CHARACTERIZATION AND DETERMINATION OF THE INHERITANCE OF CUTICLE CRACKING (RAIN CHECK) IN THE CULTIVATED TOMATO (*LYCOPERSICON ESCULENTUM*, MILL.)

By

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Dedicated to my children,

Sarah and Michael,

in appreciation of their

love and patience

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Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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Major Department: Horticultural Science

Resistance and susceptibility to cuticle cracking (CC) in tomato cultigens (genotypes) were clearly identified and could be most easily distinguished by incidence. When tested over 2 years, the amount of rain within 2 weeks prior to harvest was more highly correlated with incidence than were the amount of rain within 1 week of harvest or during the entire growing season prior to harvest.

Susceptible cultigens had greater variation in incidence of CC than resistant cultigens, with some plants appearing resistant. Selection for resistance should be based on population rather than individual plant performance. In segregating populations, plants appearing

resistant should undergo progeny testing to verify resistance.

Diallel analyses over 2 years indicated that additive gene effects were significant over all environmental conditions, with dominance effects, in the form of resistance, becoming significant under high environmental stress. Dominant alleles for resistance were evident under low to moderate environmental induction conditions. Under high environmental stress dominant alleles increased or decreased resistance. GCA was significant at all harvests, with SCA becoming significant under high environmental stress. Narrow sense and broad sense heritabilities for incidence of CC ranged from 0.45 to 0.69 and 0.62 to 0.89, respectively, increasing directly with environmental stress. Maternal effects were not significant for 3 harvests of 12 resistant by susceptible crosses, but the incidence of CC of the 'C-28' x Fla. 7181 hybrid with resistant 'C-28' as the female was significantly lower at 1994 harvest 3 than its reciprocal.

Resistant cultigens had epidermal plus cuticle (epicarp) layers significantly thicker than susceptible cultigens. Thickness of the epicarp was negatively correlated (r=-0.43) with light reflectance, and can be indirectly estimated by measuring light reflectance of the fruit. As fruit size increased, incidence of CC significantly increased, accounting for 16-33% of the

variance in incidence of CC over 2 harvests. Yield and number of fruit harvested accounted for less than 10% of the variance in incidence. Plants producing globe-shaped fruit or jointless pedicels tended to have higher incidences of CC than plants producing flat-round fruit or jointed pedicels, respectively, but this trend was significant for only one of four segregating populations for each trait.

CHAPTER 1
INTRODUCTION

Cuticle cracking is a disorder affecting tomato (*Lycopersicon esculentum*, Mill.) fruit grown under field conditions, causing a degradation of fruit appearance and reduction of shelf life (Hayman, 1987). Other names for this disorder are rain check, russeting, crazing, swell cracking, shrink cracking, hair cracking, and cuticle blotch. Cuticle cracking seems to occur when growing conditions, such as rainfall and temperature, change suddenly (Hayman, 1987). Tomato fruit are most susceptible to cuticle cracking at the mature-green stage (Young, 1947) two to three weeks prior to breaker (den Outer and van Veenendaal, 1987). Greenhouse grown tomatoes also exhibit a similar reaction to changes in growing conditions, though whether this phenomenon is the same as cuticle cracking under field conditions is not known (Ehret et al., 1993). Both of these disorders are characterized by hair-like cracks in the cuticle covering all or a portion of the calyx end, and may extend down the sides of the fruit (Hayman, 1987; Young, 1947). In more severe forms, these cracks may penetrate to the epidermal wall to form lenticel-like lesions characterized by suberin production by a repair

mechanism (Faust and Shear, 1972; Tukey, 1959). Little is known about what causes a particular variety to be resistant or susceptible to the formation of these cuticular cracks, but some information is available concerning the physiological and anatomical factors that increase the occurrence of this and other types of cracking (radial and concentric) in tomatoes and other fruiting crops.

Cracking of any type causes a degradation in fruit appearance and allows for the introduction of pathogens and a loss of water that reduce shelf life (Hayman, 1987; Reynard, 1951). Fruit with severe cases of cuticle cracking would be removed at grading stations, immediately reducing profit. Fruit with slight cuticle cracking may not be detected at grading but may have reduced shelf life. Furthermore, these fruit could act as a source of inoculum for pathogens while fruit are in storage. The economic impact of cuticle cracking may be increasing with the introduction of extended shelf life tomato varieties, since more fruit are being left on the plant beyond the mature-green stage. This practice increases the possibility that the fruit will be exposed to conditions that induce cuticle cracking and allow for pathogen introduction. Knowledge about breeding for resistance is also needed since little is known about the selection for resistance in inbred lines and how that resistance may be transferred to F_1 hybrids that are widely grown today.

The primary purpose of this study was to investigate the mode of inheritance of resistance to cuticle cracking in tomatoes by means of a diallel study. The secondary purpose of this study was to identify anatomical and/or physiological characteristics of the plant and/or fruit that are associated with resistance to this disorder.

CHAPTER 2
IDENTIFICATION OF TOMATO CULTIGENS RESISTANT AND SUSCEPTIBLE TO CUTICLE CRACKING

Introduction

Many of the factors affecting the occurrence of cuticle cracking are involved with fruit expansion due to increased water uptake and transport to the fruit. Expansion due to osmotic changes in the fruit has been demonstrated to produce sufficient pressure on the cuticle and epidermis of tomatoes and cherries to cause them to produce radial, concentric, and cuticular cracks (Batal et al., 1970; Brown and Price, 1934; Glenn and Poovaiah, 1989; den Outer and van Veenendaal, 1987). Internal turgor pressure may be generated by a variety of cultivation practices. A reduction in transpirational tissue could lead to increased water flow to the fruit. This condition may be attained and has been shown to induce cuticle cracking by pruning the plant to a single stem (Frazier, 1936) or removal of trusses of fruit (Ehret et al., 1993).

Descriptive studies indicated that cuticle cracking, as well as other types of cracking, occurred widely after periods of high rainfall (Reynard, 1951; Young, 1947) or increased irrigation (Vincent and Malenaar, 1951). Under

greenhouse conditions daily irrigation produced 22% less cracking in susceptible varieties than did watering when needed (Abbott et al., 1985). Periods of water stress have been shown to cause the epidermal cell walls of prune fruit to thicken and stiffen, making them less flexible (Milad and Shackel, 1992). This made the skin more susceptible to failure when subjected to high turgor pressures created during times of extended watering or heavy rains.

Decreasing the osmotic potential of the fruit can lead to an increased tendency of water to flow into the fruit resulting in cuticular and epidermal stretching and cracking. High light conditions may lead to high photosynthetic activity in field-grown tomatoes, and therefore, produce more sugars to be translocated to the fruit and decrease the osmotic potential (Ehret et al., 1993; Winsor and Adams, 1976). Tomato fruits grown under high light had an increased growth rate (Guan and Janes, 1991), which may or may not influence cracking.

Reports on various forms of fruit cracking were used to design a screening system for identification of resistance or susceptibility to cuticle cracking in tomato cultigens (cultivars, varieties, and breeding lines) (Soule, 1985). Past studies (Ehret et al., 1993; Frazier, 1936) indicated that increased cracking was related to removal of vegetative or reproductive tissue and exposure of fruit to intense

sunlight. Therefore, cultigens could be screened for cuticle cracking resistance or susceptibility by 1) limiting the number of fruit per truss or per plant; 2) pruning leaves to limit the leaf/shoot ratio and exposing fruit to the sun; or 3) a combination of 1 and 2.

Materials and Methods

Several genotypes (cultigens) showing variable levels of resistance or susceptibility to cuticle cracking in past work were included in this study. Plants were subjected to conditions that had been reported to induce cuticle cracking in past experiments and growing seasons, eg., pruning leaves and fruit, exposing fruit to sunlight, growing during periods of variable rainfall. Resistance or susceptibility was assigned according to the percentage of fruit affected by the disorder (incidence) and the severity of cuticle cracking on a scale from 1 to 10 (Appendix A, Figure 2-1). Cultigens with low incidences of affected fruit and low severity ratings were considered resistant, whereas those with a high incidence of affected fruit and/or high severity ratings were considered susceptible.

Spring 1992 experiment. Each cultigen (Appendix B-1) was seeded in the greenhouse in Black Beauty spent coal (Reed Minerals Div., Highland, IN) medium on 16 January and

transplanted into Todd planter flats (3.8-cm^3 cell size) (Speedling, Sun City, FL) containing a 1:1 peat and vermiculite mixture on 1 February. Plants were set into the field at the Gulf Coast Research and Education Center, Bradenton, Fla. on 6 March in a split-plot design. Each of 4 blocks had 24 plots each containing 5 to 6 plants of a cultigen (main plot). Plots were randomly arranged in 6 rows of 4 plots each. One plant per plot served as a control while three others were subjected to one of the following treatments (sub plots): exposed, limited, limited and exposed. In the exposed treatment trusses of fruit were exposed to direct sunlight by trimming leaves from around them. The limited treatment involved trimming fruit to 3 per truss. The limited and exposed treatment was a combination of the above two treatments. Mature-green and riper fruit were harvested on 5 June from 3 trusses per plant and affected fruit were rated for severity. The incidence per plant was then calculated. Severity was determined using a scale from 1 to 10 based on the proportion of surface area covered by visible cuticle cracking (Appendix A) (Figure 2-1). An index of cuticle cracking was produced by calculating the mean severity of all fruit including those not affected. The data were transformed with the square root function to improve homogeneity of the variances (Zar, 1984). Analyses of variance for incidence and severity of cuticle cracking, and

cuticle cracking index were analyzed for cultigen, block, and treatment effects as well as all interaction effects using the PROC GLM procedure of the Statistical Analysis System (SAS Institute, 1979). Multiple range tests were performed using the Means/Duncans statement of PROC GLM (SAS Institute, 1979).

Spring 1993 experiment. The objectives of this experiment were to confirm the results for selected cultigens obtained from the 1992 experiment. Cultigens Fla. 7181, 'Suncoast' (Scott et al., 1985), Fla. 7497, 'FM-9' (Leeper and Cox, 1986), 'C-28' (Moore, 1971), and Wild were seeded in the greenhouse in Black Beauty spent coal (Reed Minerals Div., Highland, IN) medium on 4 January and transplanted into Todd planter flats (3.8-cm^3 cell size) (Speedling, Sun City, FL) containing a 1:1 peat and vermiculite mixture on 19 January. Plants were set into the field at the Gulf Coast Research and Education Center, Bradenton, Fla. on 23 February in a randomized complete-block design. Each of 5 blocks contained 6 plants per cultigen in single plots. Plots were randomly arranged in 6 rows per block. All plants that were damaged due to a cold wind storm were replanted on 18 March. The breeding line designated Wild was derived as an F_1 of a cross of *L. esculentum*, Mill. with a line derived from a cross of *L. esculentum*, Mill. with *L. chilense*. This line had an extreme form of cuticle cracking under field conditions and

so was included in this experiment as a very susceptible line. Seven fruit per plant were harvested from early trusses (set before seasonal rains began) and mid-season trusses (set after seasonal rains began) and rated for severity using the scale given in Appendix A-1 and illustrated in Figure 2-1. The data were transformed with the square root function to improve homogeneity of the variances (Zar, 1984). Analyses of variance for incidence and severity of cuticle cracking, and cuticle cracking index, were analyzed for block, cultigen, and harvest effects as well as interaction effects using the PROC GLM procedure of the Statistical Analysis System (SAS Institute, 1979). Multiple range tests were performed using the Means/Duncans statement of PROC GLM (SAS Institute, 1979).

RESULTS

Spring 1992 experiment. Analysis of variance indicated that treatment (removal of leaves, fruit, or both) did not significantly affect incidence, severity, or index of cuticle cracking (Table 2-1). Cultigen effects were significant ($p<0.001$) for incidence and index but not for severity of cuticle cracking. Cultigen-by-treatment interaction effects were significant for cuticle cracking

index ($p<0.001$). Analysis by cultigen indicated that the significant interaction was due to significant ($p=0.005$) treatment effects for 'Suncoast'.

Figure 2-1. Illustration of severity of cuticle cracking rating scale.

For 'Suncoast', removal of leaves and fruit resulted in a significantly higher index of cuticle cracking than all other treatments. Treatment had no significant effects for any other cultigen.

Cultigens Fla. 7181 and 'Suncoast' had the highest incidences, whereas 'C-28', 'FM-9', and Fla. 7497 had the lowest incidences of cuticle cracking (Table 2-2). Mean severity of affected fruit ranged from 6.00 to 2.99 (Table 2-2). The Multiple Range test indicates that cultigen Fla. 7497 had a significantly ($p \leq 0.05$) higher severity rating than all other cultigens. The rating for Fla. 7497 is based on only one affected fruit and overall, cultigen did not significantly affect severity. Cuticle cracking index separated the cultigens into two groups. Fla. 7181, 'Suncoast', and 'NC50-7' rated significantly higher than all other cultigens, which were not significantly different from each other.

Spring 1993 experiment. Harvest did not have a significant effect on incidence, severity, or index of cuticle cracking (Table 2-3). Cultigen significantly affected all three measures of cuticle cracking. Cultigen effects on severity of cuticle cracking was due only to the significant difference of cultigen Wild (Table 2-5). All other cultigens had similar cuticle cracking severity.

Table 2-1. Analyses of variance for incidence, severity, and index of cuticle cracking (1992).

INCIDENCE[z]

Source	df	MS	P value
Block	3	0.08	0.15
Cultigen	10	0.37	<0.001
Error a	30	0.06	
Treatment	3	0.03	0.51
Cultigen*Treatment	30	0.05	0.43
Error b	9	0.02	
Total	85		

SEVERITY[y]

Source	df	MS	P value
Block	3	0.04	0.61
Cultigen	10	0.15	0.13
Error a	15	0.11	
Treatment	3	0.15	0.16
Cultigen*Treatment	19	0.15	0.12
Error b	9	0.05	
Total	59		

INDEX[x]

Source	df	MS	P value
Block	3	0.20	0.16
Cultigen	10	1.12	<0.001
Error a	30	0.18	
Treatment	3	0.11	0.40
Cultigen*Treatment	30	0.19	0.03
Error b	9	0.04	
Total	85		

[z] % Fruit affected per plant
[y] Mean for all affected fruit per plant
[x] Mean for all fruit per plant

Table 2-2. Incidence, severity, and index of cuticle cracking in Spring 1992 at Bradenton, Florida.

Cultigen	Incidence[z]	Severity[y]	Index[x]
Fla. 7181	28.2 ± 1.8a[w]	2.63 ± 0.67b	0.79±0.68a
Suncoast	26.6 ± 2.5a	2.99 ± 1.33b	0.94±1.15a
NC50-7	18.4 ± 1.5ab	2.99 ± 1.43b	0.58±0.59a
Fla. 7236 x CL5915 F_3	11.5 ± 1.6bc	2.21 ± 0.91b	0.22±0.32b
Fla. 7060	9.7 ± 1.2bc	2.24 ± 0.30b	0.23±0.31b
Solar Set	6.9 ± 1.1cd	2.35 ± 0.49b	0.17±0.28b
Fla. 7232B x Fla. 7321 F_4	5.4 ± 0.8cd	1.75 ± 0.61b	0.10±0.19b
Fla. 7171	4.0 ± 0.5cd	2.67 ± 1.37b	0.10±0.15b
C-28	2.4 ± 0.7cd	2.25 ± 1.77b	0.05±0.14b
FM-9	1.1 ± 0.3d	3.00 ± 1.41b	0.03±0.10b
Fla. 7497	0.7 ± 0.3d	6.00 ± 0.00a	0.04±0.17b

[z] % Fruit affected±std. deviation
[y] Per plant mean±std. deviation
[x] Mean of all fruit±std. deviation
[w] Mean (square root transformed) separation in columns by Duncan's multiple range test at $P \leq 0.05$

Significant cultigen-by-harvest interaction effects for incidence and index were due to significant differences by harvest for cultigens Fla. 7181 and Fla. 7497. Incidence and index in harvest 1 were significantly greater than for harvest 2 for Fla. 7181, whereas for Fla. 7497 harvest 2 incidence and index were significantly greater than for harvest 1. For all other cultigens harvest means were not significantly different, but the trend was for harvest 2 means to be greater than harvest 1 with the exception of 'C-28'.

Incidence of cuticle cracking for 'Suncoast' and Wild were not significantly different from each other and were significantly greater than all other cultigens (Table 2-4).

Table 2-3. Analysis of variance for incidence, severity, and index of cuticle cracking (1993).

INCIDENCE[z]

Source	df	MS	P value
Block	4	0.23	0.12
Cultigen	5	1.87	<0.001
Error a	20	0.11	
Harvest	1	0.04	0.40
Cultigen*Harvest	5	0.32	<0.001
Error b	4	0.04	
Total	225		

SEVERITY[y]

Source	df	MS	P value
Block	4	0.01	0.98
Cultigen	5	0.62	<0.001
Error a	13	0.08	
Harvest	1	0.02	0.66
Cultigen*Harvest	4	0.07	0.58
Error b	4	0.08	
Total	66		

INDEX[x]

Source	df	MS	P value
Block	4	0.80	0.10
Cultigen	5	4.32	<0.001
Error a	20	0.35	
Harvest	1	0.41	0.08
Cultigen*Harvest	5	0.92	<0.001
Error b	4	0.06	
Total	225		

[z] % Fruit affected per plant
[y] Mean for all affected fruit per plant
[x] Mean for all fruit per plant

Table 2-4. Incidence and severity of cuticle cracking in Spring 1993 at Bradenton, Florida.

Cultigen	Incidence[z]	Severity[y]	Index[x]
Wild	46.0 ± 45.9a[w]	4.26 ± 1.96a	1.97±2.38a
Suncoast	32.8 ± 2.3a	1.78 ± 0.67b	0.62±0.61b
Fla. 7181	20.8 ± 2.5b	1.98 ± 0.56b	0.42±0.55c
Fla. 7497	7.2 ± 1.2c	1.63 ± 0.58b	0.12±0.20d
FM-9	1.5 ± 0.6d	1.50 ± 0.50b	0.02±0.10d
C-28	0.8 ± 0.4d	1.50 ± 0.71b	0.12±0.06d

[z] % Fruit affected±std. deviation
[y] Per plant mean±std. deviation
[x] Mean of all fruit±std. deviation
[w] Mean (square root transformed) separation in columns by Duncan's multiple range test at $P \leq 0.05$

Fla. 7181 was significantly greater than Fla. 7497, which was significantly greater than 'C-28' and 'FM-9'. Severity of cuticle cracking fell into two groups: Wild (most affected), and all other cultigens (Table 2-4). For index of cuticle cracking Wild was greater than 'Suncoast', which was greater than Fla. 7181, which was greater than all other cultigens (Table 2-4).

Discussion

Spring 1992 experiment. Severity of affected fruit did not differ significantly between the 11 cultigens chosen for analysis; therefore, selection of cultigens for further study was based upon the incidence of cuticle cracking.

Cultigens Fla. 7181 and 'Suncoast' were the most susceptible with greater than 26% affected fruit, whereas cultigens 'C-28', 'FM-9', and Fla. 7497 were highly resistant, with less than 5% of the fruit affected. Removal of leaves, fruit, or both did not significantly affect the incidence, severity, or index of cuticle cracking over all cultigens tested. Those treatments had been shown to induce radial and cuticle cracking in tomatoes (Ehret et al., 1993; Frazier, 1936), and may not have been severe enough in our study to attain the same results.

Removal of leaves and fruit significantly increased the index of cuticle cracking for 'Suncoast', indicating that susceptible lines may be more sensitive to cultural practices than resistant lines. In addition to significant cultigen by environment interactions, susceptible cultigens showed greater variability (standard deviation) in incidence of cuticle cracking. This is similar to results from Reynard (1951) in which cultigens susceptible to radial cracking showed greater variability of response to environmental conditions than resistant cultigens.

The cultigens Fla. 7181 and 'Suncoast' (susceptible) and 'C-28', 'FM-9', and Fla. 7497 (resistant) were chosen for further study because of the significantly different levels of resistance to cuticle cracking and diverse genetic backgrounds. 'Suncoast' and Fla. 7497 have globe-shaped fruit (Appendix D) and differ in resistance to cuticle

cracking. Fla. 7181 produces flat-round fruit with jointless pedicels (Appendix D). Fla. 7497 has an arthritic type pedicel in which the pedicel above the abscission zone is swollen and does not cleanly separate from it. 'FM-9' is resistant to cuticle cracking, producing "deep-round" fruit with a "square appearance" (Leeper and Cox, 1986), with jointed pedicels. 'C-28' is very resistant to cuticle cracking and produces flat-round fruit with jointed pedicels.

Spring 1993 experiment. Ranking of the cultigens from most susceptible to most resistant based on incidence did not deviate greatly from the 1992 season. 'Suncoast' and Fla. 7181 were susceptible, whereas Fla. 7497, 'C-28', and 'FM-9' had greater resistance. All three resistant cultigens showed higher incidence of the disorder in 1993 than in 1992, suggesting a season with greater stress factors for cuticle cracking. As in the 1992 season, severity did not differ significantly between these five cultigens, and was very low (less than 2). This suggests that incidence of cuticle cracking is more important in selection of resistant lines for breeding than severity. Once cuticle cracking is expressed the level of severity does not vary. Therefore, resistance to cuticle cracking refers to the ability of a plant to produce fruit on which cuticle cracking is rarely induced.

The Wild cultigen had the highest incidence of cuticle cracking, as well as having the highest severity rating. The visible appearance of the cuticle cracking in this cultigen is not the same as in the pure L. esculentum lines (Figure 2-2) and is suspected to be a disorder different from cuticle cracking.

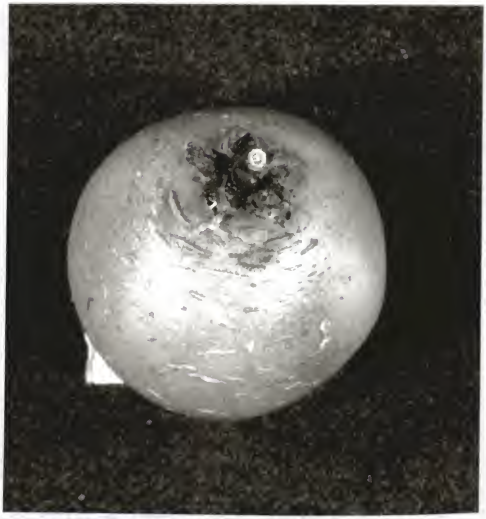


Figure 2-2. Cuticle cracking of cultigen 'Wild'.

CHAPTER 3
ENVIRONMENTAL FACTORS INFLUENCING INCIDENCE AND SEVERITY OF CUTICLE CRACKING

Introduction

Fruit expansion occurs as a result of increased water influx to the fruit, generating turgor pressure (Cosgrove, 1986). This may be due to increased osmotic pressure in the fruit tissue as sugars and organic acids are produced or increased water potential at the root/soil interface. Either situation creates an osmotic gradient at the root zone, allowing for water influx. Different types of fruit cracking have been reported to occur under field conditions after periods of heavy rainfall that would increase the root/soil water potential gradient (Reynard, 1951; Young, 1947). Irregular watering regimes in the greenhouse have also been indicated to increase cracking (Abbott et al., 1985). High soil conductivity and low night-time relative humidity contributed to low cuticle cracking (Ehret and Helmer, 1995), potentially by creating situations in which transpiration rates were altered and tissue water potential and growth were reduced (Cosgrove, 1986). High relative humidity has been shown to increase susceptibility of apples

to russetting by inhibiting the production of a thick cuticle (Faust and Shear, 1972).

Altering soil conductivity or relative humidity in a field situation is a difficult undertaking. The spring rainfall patterns in west-central Florida create a growing season in which fruit from the same plant may expand and mature under different levels of rainfall and, therefore, differing soil conductivities and osmotic gradients. Early in the season there is typically little rainfall and low relative humidity, producing conditions that would lead to low levels of cuticle cracking. As the season progresses the amount of rainfall and the relative humidity both increase, thereby increasing the water available for transport and increasing the potential for cuticle cracking to occur.

In this study rainfall events and amounts near harvest were monitored over 2 years to estimate their importance in the induction of cuticle cracking in resistant and susceptible cultigens (cultivars, varieties, and breeding lines) (Soule, 1985).

Materials and Methods

Spring 1994 experiment. Cultigens 'C-28', 'FM-9', Fla. 7497, 'Suncoast', and Fla. 7181 were seeded in the

greenhouse in Black Beauty spent coal (Reed Minerals Div., Highland, IN) medium on 24 January and transplanted into Todd planter flats (3.8-cm^3 cell size) (Speedling, Sun City, FL) containing a 1:1 peat and vermiculite mixture on 7 February. Plants were set into the field at the Gulf Coast Research and Education Center, Bradenton, Fla. on 8 March in a randomized, complete-block design. Cultigens not used in this analysis were included in the field. Each of 4 blocks had 30 plots containing 8 plants of an individual line. Plots were arranged randomly in 6 rows per block. Mature-green and riper fruit were harvested from all plants per plot on 6 June before seasonal rains (1994H1), 13 June after moderate rain (1994H2) and 20 June after a significant amount of rainfall (1994H3) (See Table 3-1). Incidence and severity of cuticle cracking were determined for each cultigen on a per plot basis. Severity was determined using a scale from 1 to 10 based on the proportion of surface area covered by visible cuticle cracking (Appendix A). The data were transformed using the square root function to make the variances homogeneous (Zar, 1984). Incidence, severity, and index of cuticle cracking were analyzed by PROC GLM and PROC CORR procedures of the Statistical Analysis System (SAS Institute, 1979). Multiple range tests were performed using the Means/Duncans statement of PROC GLM (SAS Institute, 1979).

Spring 1995 experiment. The same cultigens used for analysis as in 1994 were seeded in the greenhouse in Black Beauty spent coal (Reed Minerals Div., Highland, IN) medium on 23 January and transplanted into Todd planter flats (3.8-cm^3 cell size) (Speedling, Sun City, FL) containing a 1:1 peat and vermiculite mixture on 8 February. Plants were set into the field at the Gulf Coast Research and Education Center, Bradenton, Fla. on 8 March in a randomized, complete-block design. Cultigens not used in this analysis were included in the field. Each of 4 blocks had 15 plots, containing 8 plants of an individual cultigen. Plots were randomly arranged in 6 rows per block. Mature-green and riper fruit were harvested on an individual plant basis between 30 May and 5 June before seasonal rains (1995H1) and between 12 and 16 June after a significant amount of rainfall (1995H2). Incidence, severity, and index of cuticle cracking were determined for each cultigen on a per plant basis. The data were analyzed as for the 1994 season. Rainfall amounts from planting to harvest, two weeks prior to harvest, and one week prior to harvest were tested for correlations with incidence, severity, and index of cuticle cracking using the PROC CORR procedure of the Statistical Analysis System (SAS Institute, 1979).

RESULTS

Rainfall amounts for the 1994/95 harvests are in Table 3-1 along with incidence, severity, and index of cuticle cracking for the 5 cultigens tested. In both years incidence and index of cuticle cracking increased with each harvest. Severity was relatively stable over 3 harvests in 1994 and increased over 2 harvests in 1995. Severity at 1994H1 was based on a low number of affected fruit (less than 10 for most cultigens tested) and so was considered to be an unreliable estimate. When this was taken into consideration severity of affected fruit increased with each harvest for each year of the study.

The harvests may be ranked from low to high stress conditions according to the incidence or index of cuticle cracking. 1994H1 was not significantly different from 1995H1. 1994H2 was greater than 1994H1 and 1995H1, but less than 1994H3. 1995H2 and 1994H3 were not significantly different from each other, but were significantly greater than 1994H2 (Table 3-1) ($p \leq 0.05$). Ranking of harvests by severity from low to high is as follows: 1994H2, 1995H1, 1994H3, 1995H2 ($p \leq 0.05$). 1994H1 data was not included in this ranking due to very low numbers of affected fruit (less than ten for most cultigens). 1995H1 severity was greatly inflated due to the mean of 'FM-9' (data not shown).

Removal of this cultigen from analysis brings the mean of 1995H1 to 1.24 and alters the ranking of harvests from low to high to: 1995H1, 1994H2, 1994H3, 1995H2.

Table 3-1. Rainfall and cuticle cracking data for 1994 and 1995.

YEAR	1994			1995	
HARVEST	1 (6/6)	2 (6/13)	3 (6/20)	1 (5/30)	2 (6/5)
RAINFALL(cm)					
PLANT TO HARVEST	11.0	16.4	29.7	18.8	33.1
2 WEEKS PRIOR[z]	1.6	7.0	18.8	3.8	14.3
1 WEEK PRIOR[z]	1.6	5.4	13.3	3.2	2.8
INCIDENCE[y]	4.9c[v]	24.0b	34.1a	4.2c	26.3ab
SEVERITY[x]	4.08b	2.79c	3.41b	3.22d	4.88a
INDEX[w]	0.20c	0.77b	1.26a	0.06c	1.26a

[z] Prior to harvest
[y] % Fruit affected over all cultigens
[x] Mean for all affected fruit
[w] Mean severity for all fruit
[v] Mean separation in rows by Duncan's multiple range test at $P \leq 0.05$. Data were transformed to square roots before analysis.

Rainfall from planting to harvest was not significantly correlated to incidence and index of cuticle cracking (Table 3-2). Rainfall within two weeks prior to harvest was highly correlated to incidence and index of cuticle cracking. Rainfall levels within one week prior to harvest were not significantly correlated to incidence, severity, or index of cuticle cracking (Table 3-2). Severity of affected fruit

was not correlated to rainfall during any of the time periods tested, even with 1994H1 removed from the analysis (data not shown). With the extreme cultigen ('FM-9') removed from 1995H1 the tendency was for severity to increase with rainfall from planting to harvest.

Table 3-5. Pearson correlation coefficients and probabilities[z] for rainfall and cuticle cracking measures.

	PLANT TO HARVEST	2 WEEKS PRIOR	ONE WEEK PRIOR
INCIDENCE[y]	0.74 (0.15)	0.92 (0.03)	0.73 (0.16)
SEVERITY[x]	0.44 (0.46)	0.21 (0.73)	-0.38 (0.53)
INDEX[w]	0.84 (0.08)	0.93 (0.02)	0.59 (0.30)

[z] in ()
[y] % Fruit affected
[x] Mean for all affected fruit
[w] Severity mean for all fruit

DISCUSSION

One study of cuticle cracking in tomatoes has indicated that the incidence of this disorder shows a positive relationship to rainfall (Young, 1947), but this relationship has not been directly tested. Reynard (1951) reported that the incidence of radial cracking in tomatoes

was related to the number of days of rain prior to harvest, but not to the amount of rain. The results of this study clearly indicated that the amount of rainfall occurring within two weeks of harvest was significantly correlated to the incidence of cuticle cracking. This two-week time frame coincides with the end of the second growth stage of tomato fruit and the time at which the majority of fruit are harvested. This stage is characterized by rapid cell expansion driven by turgor pressure, leading to increased cell and fruit volume (Rudich and Luchinsky, 1986). Bakker (1988) reported that cuticle cracking typically occurred 6 to 7 weeks after fruit set (within our 2 week rainfall time frame) and severity was significantly correlated with growth rate. As the fruit approach the mature-green stage and ripening is initiated, the elasticity of the epidermis decreases (Kamimura et al., 1972). Cultigens most susceptible to cracking were found to be those with low epidermal elasticity (Kamimura et al., 1972). Under moderate water deficit conditions, many tissues will produce more reducing sugars and organic acids to increase the osmotic gradient and maintain turgor (Cosgrove, 1986). This could lead to cuticle cracking if turgor pressure is increased rapidly due to the occurrence of a heavy rainfall. The cells would expand rapidly, placing extreme pressure on the epidermis and cuticle. Limited epidermal elasticity

and/or weaknesses in the cuticular layer would then lead to cracking.

Severity of cuticle cracking for affected fruit was less sensitive to rainfall patterns than incidence or index. The tendency was for severity to increase with each harvest. This higher variability resulted in a nonsignificant correlation, making severity less predictable and, therefore, less reliable as an indicator of resistance to cuticle cracking due to environmental conditions. Index of cuticle cracking was based on incidence and severity. It is a better indicator of resistance to cuticle cracking due to environmental conditions than severity, but gives no more information than incidence. Incidence of cuticle cracking is simpler and quicker to measure and, thus, is the best indicator of sensitivity due to environmental conditions.

CHAPTER 4
THE INHERITANCE OF RESISTANCE TO CUTICLE CRACKING IN TOMATO

Introduction

Cuticle cracking (rain check) in tomato (*Lycopersicon esculentum,* Mill.) is characterized by hair-like cracks in the cuticular layer of the fruit that may penetrate to the epidermal wall, resulting in suberization. Those cracks are generally located on the shoulders of the fruit, but occasionally extend down the sides and even cover the entire fruit surface. The disorder occurs under both field and greenhouse conditions, often leading to significant economic losses to the fresh market tomato industry (Hayman, 1987). Environmental factors such as rainfall or irrigation practices (Abbott et al., 1985), soil conductivity (Hayman, 1987), low night temperature (Hayman, 1987), and high relative humidity (Ehret et al., 1993) have been associated with the occurrence of cuticle cracking. Anatomical and physiological factors have also been identified that influence the occurrence of cuticle cracking in tomato and other fruit. Studies on the effect of fruit size on the occurrence and severity of cuticle cracking have been in conflict. Studies by Janse (1985) and Koske et al. (1980) agreed with the theoretical studies of Considine and Brown

(1981), indicating that larger fruit were more susceptible to cuticle cracking than small fruit. In opposition to this, Bakker (1988) and Ehret et al. (1993) found that large fruit were less susceptible, or that size was not a factor in cuticle cracking. Theoretically, deviations from spherical shape would alter the distribution of forces generated by turgor pressure, placing greater pressure on one area of the fruit wall (Considine and Brown, 1981). Therefore, fruit shape may play a role in inducing cuticle cracking. The force generated by turgor is placed upon the epidermal wall and cuticle. Thin cuticles are partly responsible for the occurrence of cuticle cracking (russeting) in apples (Bell, 1937; Tukey, 1960). Similar results have been published for radial and concentric cracking in tomato (Hankinson and Rao, 1979; Voisey et al., 1970), and thin cuticles were suspected to be a factor in cuticle cracking (den Outer and van Veenendaal, 1987).

Leaf cover of a plant may act to shade the fruit, thus reducing diurnal expansion due to temperature (Cockshull et al., 1992) and preventing altered polymerization of the cuticular waxes by UV radiation (Vries, 1970). Vegetative tissue also acts as a transpirational surface, reducing the amount of water flowing to fruit.

Studies on the relationship between growth rate and cracking (concentric, cuticle, or radial) have conflicting results. Bakker (1988) reported that tomato fruits with

high growth rates near the end of the growth period showed more cuticle cracking than those with low growth rates. Ehret et al. (1993) found no relationship between long term growth rate and cuticle cracking. Frazier and Bowers (1947) reported that radial and concentric cracking occurred after the period of high growth rate. Those discrepancies may exist due to the differing methods of determining growth rate and the type of cracking measured.

Fruit pruning, resulting in fewer fruit developing at a given harvest, increased cuticle cracking in tomato (Ehret et al., 1993). This may have been the result of increased water flow to remaining fruit.

Genetic studies of cracking in tomato have been done on radial and concentric cracking, but not cuticle cracking. Radial and concentric cracking are controlled by different gene systems with genes unique to each type of cracking (Avdeyeev, 1979; Cortes et al., 1983; Frazier, 1952; Hudson, 1955; Gill and Nandpuri, 1970; Young, 1958; Young, 1963). Frazier (1936) reported that those two types of cracking may occur at different times of the growing season and under different conditions. Cuticle cracking also occurs independently from either of these other types of cracking, suggesting that it is controlled by another gene system.

The objective of this study was to obtain information on the inheritance of resistance to cuticle cracking by diallel analyses conducted over two seasons. Such

information was considered relevant considering the importance of F_1 hybrids presently used in commercial production.

Materials and Methods

Based upon the results of Spring 1992 and Spring 1993 experiments five cultigens (cultivars, varieties, and breeding lines) (Soule, 1985) were chosen for genetic studies. Cultigens Fla. 7181 and 'Suncoast' (Scott et al., 1985) were selected as susceptible parents, whereas Fla. 7497, 'FM-9' (Leeper and Cox, 1986), and 'C-28' (Moore, 1971) were chosen as resistant parents. 'Suncoast' and Fla. 7497 have globe-shaped fruit (Appendix D) and differ in resistance to cuticle cracking. Fla. 7181 produces flat-round fruit with jointless pedicels (Appendix D). Fla. 7497 has an arthritic type pedicel in which the pedicel is swollen above the abscission zone and does not separate from it cleanly. 'FM-9' produces "deep-round" fruit with a "square appearance" (Leeper and Cox, 1986), with jointed pedicels. 'C-28' produces flat-round fruit with jointed pedicels. The five cultigens were reciprocally intercrossed in 10 combinations to produce 20 F_1 hybrids.

Spring 1994 full diallel. Each cultigen (Appendix B-3) was seeded in the greenhouse in Black Beauty spent coal

(Reed Minerals Div., Highland, IN) medium on 24 January and transplanted into Todd planter flats (3.8-cm^3 cell size) (Speedling, Sun City, FL) containing a 1:1 peat and vermiculite mixture on 7 February. Plants were set into the field at the Gulf Coast Research and Education Center, Bradenton, Fla. on 8 March in a randomized, complete-block design. Each of 4 blocks had 30 plots containing 8 plants of an individual parental or F_1 hybrid line. Cultigens not used in this analysis were included in the field. Plots were randomly arranged in 6 rows per block. Mature-green and riper fruit were harvested from all plants per plot on 6 June before seasonal rains (1994H1), 13 June after moderate rain (1994H2) and 20 June after a significant amount of rainfall (1994H3). Incidence and severity of cuticle cracking were determined for each cultigen and the data were transformed using the square root function to make the variances homogeneous (Zar, 1984). Severity was determined for all fruit with cuticle cracking on a scale from 1 to 10, based on the percentage of surface area covered with visible cuticular cracks (Appendix A). An index of cuticle cracking was calculated as the mean severity of all fruit on a scale from 0 to 10. Incidence, index, and severity of cuticle cracking were analyzed by PROC GLM and PROC CORR procedures of the Statistical Analysis System (SAS Institute, 1979). Means were compared by Duncan's multiple range test using PROC GLM (SAS Institute, 1979). Diallel analyses of Hayman

(1954) and Griffing (1956) were conducted on cuticle cracking incidence using a software package provided by B. R. Christie et al. (1980).

Spring 1995 half diallel. Each cultigen (Appendix B-3) was seeded in the greenhouse in Black Beauty spent coal (Reed Minerals Div., Highland, IN) medium on 23 January and transplanted into Todd planter flats (3.8-cm^3 cell size) (Speedling, Sun City, FL) containing a 1:1 peat and vermiculite mixture on 8 February. Plants were set into the field at the Gulf Coast Research and Education Center, Bradenton, Fla. on 8 March in a randomized, complete-block design. There were 4 blocks with 15 eight-plant plots, each with an individual cultigen. Plots were randomly arranged in 6 rows per block. Mature-green and riper fruits were harvested on an individual plant basis between 30 May and 5 June before seasonal rains (1995H1) and between 12 and 16 June after a significant amount of rainfall (1995H2). Data were analyzed as in the 1994 experiment.

Results

Spring 1994 full diallel. Analysis of variance indicated cultigen, harvest, and harvest by cultigen effects were significant for incidence, severity, and index of cuticle cracking (Table 4-1). Significant block effects

were due to significant differences in a single block (data not shown).

In general, cuticle cracking (CC) incidence for cultigens at harvest 3 was greater than or equal to the incidence of CC for cultigens at harvest 2, and incidence of CC for cultigens at harvest 2 was greater than or equal to the incidence of CC for cultigens at harvest 1 (Table 4-2, data for F_1 lines not shown). The significant cultigen by harvest effects for incidence were due to 'FM-9' and 'FM-9' x Fla. 7497 reciprocal F_1s having no significant differences between harvests, whereas all other cultigens had significant differences (data not shown). Due to the harvest by cultigen interaction further analyses were conducted on a by harvest basis.

On an individual harvest basis, reciprocal differences were insignificant except for the 'C-28' x Fla. 7181 F_1 hybrids at harvest 3 (Table 4-3a), where the hybrid with the resistant parent as the female had a significantly lower incidence than the reciprocal. Though overall differences due to maternal effects were not significant, the trend for most of the resistant by susceptible crosses was in the same direction as for 'C-28' x Fla. 7181, ie., hybrids with the resistant parent as female had lower incidence of CC than the reciprocal.

Table 4-1. Analysis of variance for parental and F_1 cultigens in 1994.

INCIDENCE[z]

Source	df	MS	P value
Block	3	0.08	<0.001
Cultigen	24	0.22	<0.001
Error a	72	0.02	
Harvest	2	2.87	<0.001
Harvest*Cultigen	48	0.02	0.001
Error b	6	0.02	
Total	155		

SEVERITY[y]

Source	df	MS	P value
Block	3	0.02	0.57
Cultigen	24	0.11	<0.001
Error a	72	0.04	
Harvest	2	0.38	<0.001
Harvest*Cultigen	48	0.06	<0.001
Error b	6	0.07	
Total	155		

INDEX[x]

Source	df	MS	P value
Block	3	0.29	<.001
Cultigen	24	0.89	<0.001
Error a	72	0.08	
Harvest	2	10.07	<0.001
Harvest*Cultigen	48	0.09	<0.001
Error b	6	0.07	
Total	155		

[z] % Fruit affected
[y] Mean for all affected fruit
[x] Severity mean for all fruit

Table 4-2. Incidence of cuticle cracking for parents (1994).

Cultigen	Harvest 1	Harvest 2	Harvest 3
Fla. 7181	21.8a[z]	55.7a	64.9a
Suncoast	3.1b	33.2a	35.8b
Fla. 7497	0.3b	9.9b	32.4bc
FM-9	1.0b	12.4b	22.6bc
C-28	0.1b	3.4b	15.0c

[z]Mean (square root transformed) separation in columns by Duncan's multiple range test at $p \leq 0.05$

At harvest 1, 14 of 20 reciprocal hybrids had incidences of CC less than the mid-parent (MP). Of the 12 resistant by susceptible (RxS) F_1 reciprocal hybrids, 6 had incidences not significantly different from the resistant parent, each with Fla. 7181 as the susceptible parent (Table 4-3a). Five of the RxS hybrids were intermediate to the parents, 3 of which were less than the mid-parent (MP) and 2 were greater than the MP. The 'Suncoast' x Fla. 7497 hybrid was not significantly different from 'Suncoast'. None of the 6 resistant by resistant (RxR) hybrids were significantly different from either parent, with equal numbers greater than or less than the MP. Both susceptible by susceptible (SxS) reciprocal hybrids were not significantly different from the less susceptible parent.

Table 4-3. Incidence of cuticle cracking for F_1 hybrids (1994).

a. HARVEST 1

Male / Female	C-28	FM-9	Fla. 7497	Suncoast	Fla. 7181
C-28	-	0.1	0.5[z]	1.6	5.8[y]
FM-9	0.2	-	0.2	8.2	6.8[y]
Fla. 7497	0.4[z]	1.0[z]	-	4.4[z]	8.4[y]
Suncoast	3.4[z]	1.7	6.8[zx]	-	11.6[y]
Fla. 7181	7.6[y]	5.6[y]	4.4[y]	8.2[y]	-

b. HARVEST 2

Male / Female	C-28	FM-9	Fla. 7497	Suncoast	Fla.7181
C-28	-	5.1	6.8[z]	9.1[y]	10.7[y]
FM-9	0.1	-	3.6	17.2	15.2[y]
Fla. 7497	1.7	5.4	-	17.8	14.1[y]
Suncoast	21.4[zx]	19.7	20.5	-	38.8
Fla. 7181	19.4	25.1[y]	19.5[y]	50.2[z]	-

c. HARVEST 3

Male / Female	C-28	FM-9	Fla. 7497	Suncoast	Fla. 7181
C-28	-	13.9	9.8[y]	28.4[z]	20.5[yv]
FM-9	13.9	-	4.4	24.4	32.5[y]
Fla. 7497	5.2[w]	3.1[w]	-	24.6	34.1[y]
Suncoast	24.8	32.7[z]	37.3[z]	-	60.1[z]
Fla. 7181	43.6[zx]	25.6[y]	53.3[z]	42.9	-

[z] > Mid-parent
[y] Not significantly different from more resistant parent (Table 4-2)
[x] Not significantly different from more susceptible parent
[w] Significantly less than both parents (overdominance)
[v] Significantly less than reciprocal

All 20 reciprocals had incidences intermediate to both parents, and 18 were less than the MP at harvest 2 (Table 4-3b). Six of 12 RxS reciprocal hybrids were not significantly different from the resistant parent, 5 were less than the MP, and 1 ('Suncoast' x 'C-28') was not significantly different from the susceptible parent. All 6 RxR reciprocal hybrids were intermediate to the parents, one of which was greater than the MP ('C-28' x Fla. 7497). Both SxS reciprocal hybrids were intermediate to the parents, one greater than and one less than the MP. At harvest 3, 14 of 20 reciprocals had incidences less than the MP (Table 4-3c). Four of 12 RxS reciprocal hybrids were not significantly different from the resistant parent, 3 were less than the MP, 5 were greater than the MP, with one (Fla. 7181 x 'C-28') significantly different from the reciprocal and not significantly different from Fla. 7181. Three of 6 RxR reciprocal hybrids were significantly less than both parents, one was not significantly different from the more resistant parent, and the other 2 were intermediate to the parents and less than the MP.

Cultigen, harvest and cultigen-by-harvest interactions were significant for severity of cuticle cracking (Table 4-1). Harvest 3 had significantly greater severity than harvest 1 or harvest 2 (data not shown). A significant cultigen by harvest interaction was due to only 4 out of 25 lines having significant differences between harvests.

The means for these lines ('C-28', 'FM-9', Fla. 7497, and 'C-28 x 'FM-9') were based on very few affected fruit in harvest 1 (Table 4-4), resulting in an inflated mean and making them inaccurate estimates. If harvest 1 is not considered these lines fit the overall pattern of harvest 3 having greater severity than harvest 2.

On an individual harvest basis, the designation of parents as resistant or susceptible was consistent if harvest 1 was not considered due to the low numbers of affected fruit. Cultigen Fla. 7497 was intermediate between resistant and susceptible at harvest 2, and significantly greater than the resistant cultigens at harvest 3 (Table 4-4). 'Suncoast' was susceptible at harvest 2, but not significantly different from the resistant cultigens at harvest 3 (Table 4-4).

Table 4-4. Cuticle cracking severity for parents (1994).

Cultigen	Harvest 1	Harvest 2	Harvest 3
Fla. 7181	3.91±0.80b[z]	3.48±0.44a	4.03±0.84a
Suncoast	3.50±0.71b	3.13±0.21a	3.47±0.38ab
Fla. 7497	6.00±0.00[y]a	2.72±0.65ab	3.97±0.35a
FM-9	3.00±0.00[y]b	2.22±0.28b	2.88±0.48b
C-28	6.00±0.00[y]a	2.00±0.00b	2.71±0.31b

[z] Mean separation in columns by Duncan's multiple range test at $p \leq 0.05$

[y] Mean based on one affected fruit

No consistent pattern of maternal effects was evident in the reciprocal hybrids. At harvest 1, all F_1 hybrids, except 'FM-9' x 'Suncoast', were less than the MP (Table 4-5a). Eight of 12 RxS reciprocal hybrids were not significantly different from the resistant parent, one ('FM-9' x 'Suncoast') was significantly greater than its reciprocal, and 3 were intermediate to both parents and less than the MP. Four of 6 RxR reciprocal hybrids had severities significantly lower than both parents, with the remaining 2 less than the MP. Both SxS reciprocal hybrids were intermediate to both parents and less than the MP.

Fourteen of 20 reciprocals had severity greater than the MP at harvest 2 (Table 4-5b). Four of 12 RxS reciprocals had severity not significantly different from the susceptible parent, all having 'C-28' as a parent. One ('C-28' x 'FM-9') of 6 RxR reciprocal hybrids was not significantly different from the more resistant parent, and was significantly lower than its reciprocal, 2 were intermediate to the parents and less than the MP, and 3 were intermediate to the parents and greater than the MP. Both SxS reciprocal hybrids were intermediate to the parents and greater than the MP. At harvest 3, 15 of 20 reciprocals had CC severity intermediate to the parents (Table 4-5c). Two of 12 RxS reciprocal hybrids were not significantly different from the resistant parent, one ('C-28' x 'Suncoast') was not significantly different from the

susceptible parent and was significantly greater than its reciprocal, 7 were intermediate to the parents and less than the MP, and 2 were intermediate to the parents and greater than the MP. Two of 6 RxR reciprocal hybrids were not significantly different from the more resistant parent, whereas the remaining 4 were intermediate to the parents with equal numbers greater or less than the MP.

Cultigen, harvest, and cultigen-by-harvest interactions were significant for cuticle cracking index (Table 4-1). Ranking of harvests by index from high to low was: harvest 3 was greater than harvest 2, which was greater than harvest 1. A significant cultigen by harvest interaction was due to three cultigens ('FM-9', 'FM-9' x 'Suncoast', and 'FM-9' x Fla. 7497) with no significant differences in cuticle cracking index between harvests. Over all harvests and within each individual harvest, parental line Fla. 7181 had the highest cuticle cracking index followed by 'Suncoast' (or Fla. 7497 at Harvest 3), Fla. 7497, 'FM-9', and 'C-28' (Table 4-6).

'C-28' x Fla. 7181 reciprocals were significantly different at harvest 3, with the hybrid having 'C-28' as the female parent being significantly lower than the reciprocal (Table 4-7c). No other reciprocal differences were found. Two cases of overdominance occurred at harvest 3: 'FM-9' x Fla. 7497 and Fla. 7497 x 'FM-9' were significantly lower than either parent (Table 4-7c).

Table 4-5. Cuticle cracking severity for F_1 hybrids (1994).

a. Harvest 1

Male / Female	C-28	FM-9	Fla. 7497	Suncoast	Fla. 7181
C-28	-	2.67[y]	2.55[w]	2.92[y]	2.78[y]
FM-9	3.00[y]	-	1.50[w]	4.28[v]	2.85
Fla. 7497	2.38[w]	2.00[w]	-	2.79[y]	3.09[y]
Suncoast	3.03[y]	3.15	2.82[y]	-	2.78
Fla. 7181	3.18[y]	2.60	2.56[y]	3.12	-

b. Harvest 2

Male / Female	C-28	FM-9	Fla. 7497	Suncoast	Fla. 7181
C-28	-	1.53[yv]	2.96[z]	3.02[zx]	3.29[zx]
FM-9	2.67[z]	-	2.44	2.81[z]	3.21[z]
Fla. 7497	2.79[z]	2.38	-	3.16[z]	3.16[z]
Suncoast	3.69[zx]	2.92[z]	2.84	-	3.66[z]
Fla. 7181	3.06[zx]	2.97[z]	2.87	3.53[z]	-

c. Harvest 3

Male / Female	C-28	FM-9	Fla. 7497	Suncoast	Fla. 7181
C-28	-	2.91[z]	2.60	4.33[zxv]	2.93[y]
FM-9	3.37[z]	-	3.17	2.91	2.85[y]
Fla. 7497	3.14[y]	2.67[y]	-	3.29	3.57
Suncoast	2.99	3.35[z]	3.69	-	3.91[z]
Fla. 7181	3.67[z]	3.15	3.40	4.14[z]	-

[z] > Mid-parent
[y] Not significantly different from more resistant parent (Table 4-4)
[x] Not significantly different from more susceptible parent
[w] Significantly less than both parents (overdominance)
[v] Significantly different from reciprocal

Table 4-6. Cuticle cracking index for parents (1994).

Cultigen	Harvest 1	Harvest 2	Harvest 3
Fla. 7181	0.91a[z]	1.98a	2.68a
Suncoast	0.14b	1.04a	1.23b
Fla. 7497	0.03b	0.28b	1.30b
FM-9	0.04b	0.29b	0.69bc
C-28	0.01b	0.07b	0.42c

[z] Mean separation within columns by Duncan's multiple range test at $p \leq 0.05$

At harvest 1, 6 of 12 RxS reciprocals had indices not significantly different from the resistant parent, all of which had Fla. 7181 as a parent. Of the remaining 6 RxS reciprocals, 4 were intermediate to the parents and greater than the MP, and 2 were intermediate to the parents and less than the MP. Each of the 6 RxR reciprocals were intermediate to the parents and less than the MP. Both SxS reciprocals were not significantly different from 'Suncoast'.

Seventeen of 20 reciprocals had indices less than the MP at harvest 2 (Table 4-7b). Six of 12 RxS reciprocals were not significantly different from the resistant parent, one was not significantly different from 'Suncoast', and 5 were intermediate to both parents and less than the MP. All RxR reciprocals were intermediate to the parents, with only 1 ('C-28' x Fla. 7497) greater than the MP. Both SxS reciprocals were intermediate to the parents with 'Suncoast' x Fla. 7181 less than the MP, and the reciprocal greater

than the MP. At harvest 3, 4 of 12 RxS reciprocals were not significantly different from the resistant parent, one of which ('C-28' x Fla. 7181) was significantly less than its reciprocal. One RxS reciprocal ('C-28' x 'Suncoast') was not significantly different from the susceptible parent, whereas the remaining 4 were intermediate to the parents and less than the MP. Two of 6 RxR reciprocals were significantly lower than both parents, 2 were not significantly different from the more resistant parent, and 2 were intermediate to the parents and less than the MP.

Since overall reciprocal differences were not significant, reciprocal F_1 hybrids were pooled and Hayman's (1954) and Griffing's (1956) analyses performed on a by harvest basis. Severity of cuticle cracking did not differ enough between parents to make it useful for this genetic study, and cuticle cracking index did not provide any different information than incidence. Therefore, incidence of cuticle cracking was the focus of these analyses. Results of the Hayman's analyses are in Table 4-8. Data from block 3 of harvest 3 was significantly different from that of the other blocks and rendered the analysis invalid due to non-uniformity of Wr-Vr. Therefore, block 3 data were not included in the Harvest 3 analysis. Variation due to additive gene effects (d) was significant for all harvests.

Table 4-7. Cuticle cracking index for F_1 hybrids (1994).

a. Harvest 1

Male / Female	C-28	FM-9	Fla. 7497	Suncoast	Fla. 7181
C-28	-	0.01	0.01	0.04	0.17[y]
FM-9	<0.01	-	<0.01	0.40[z]	0.21[y]
Fla. 7497	0.01	0.01	-	0.14[z]	0.16[y]
Suncoast	0.10[z]	0.05	0.19[z]	-	0.33[y]
Fla. 7181	0.28[y]	0.14[y]	0.12[y]	0.29[y]	-

b. Harvest 2

Male / Female	C-28	FM-9	Fla. 7497	Suncoast	Fla. 7181
C-28	-	0.04	0.19[z]	0.26[y]	0.34[y]
FM-9	0.08	-	0.09	0.49	0.50[y]
Fla. 7497	0.04	0.08	-	0.63	0.47[y]
Suncoast	0.91[zx]	0.58	0.58	-	1.41
Fla. 7181	0.56	0.76[y]	0.56[y]	1.80[z]	-

c. Harvest 3

Male / Female	C-28	FM-9	Fla. 7497	Suncoast	Fla. 7181
C-28	-	0.46	0.26[y]	1.19[zx]	0.56[yv]
FM-9	0.51	-	0.14[u]	0.73	0.91[y]
Fla. 7497	0.18[y]	0.05[u]	-	0.85	1.18[y]
Suncoast	0.74	1.10[z]	1.41[z]	-	2.39[z]
Fla. 7181	1.61[z]	0.81[y]	1.79	1.75	-

[z] > Mid-parent
[y] Not significantly different from more resistant parent (Table 4-6)
[x] Not significantly different from more susceptible parent
[u] Significantly less than both parents (overdominance)
[v] Significantly different from reciprocal

Table 4-8. Hayman's analysis for incidence of cuticle cracking, Spring 1994 full diallel.

Parameter	Harvest 1	Harvest 2	Harvest 3
d^z	0.003*[t]	0.0154*	0.0110*
h^{2y}	-0.0001	0.0044	0.0063*
$m_{L1} - m_{L0}$[x]	-0.0043	-0.0273	-0.0379
$(H_1/d)^{0.5w}$	0.6570	0.5629	1.0494
$(h^2/H_2)^v$	0	1	1
r for Wr+Vr and Yr[u]	0.996	0.989	0.698
NS heritability	0.54	0.63	0.69
BS heritability	0.67	0.72	0.89
C-28	D[s]	D	D
FM-9	D	D	D
Fla. 7497	D	D	R
Suncoast	D	R	D
Fla. 7181	R	R	R

[z] Additive gene effects
[y] Dominance gene effects
[x] Degree and direction of dominance
[w] Dominance type (>1=over-dominance, <1=partial dominance)
[v] Number of gene groups exhibiting dominance
[u] Correlation coefficient between parental order of dominance and parental measure (indicates reliability of gene effect estimates)
[t] An * indicates significance at $p \leq 0.05$
[s] Type of alleles more frequent: D=dominant R=recessive

Dominance effects (h^2) over all heterozygous loci in all crosses increased with each harvest, but were significant only at harvest 3. Means of the progeny minus parental means ($m_{L1} - m_{L0}$), a measure of degree and direction of dominance, were negative and increased in degree with each harvest. Accordingly, the degree of dominance was 0.66, 0.56, and 1.05 for harvests 1, 2, and 3, respectively. The number of gene groups exhibiting dominance, as indicated by (h^2/H_2) were 0, 1, and 1, for harvests 1, 2, and 3,

respectively. High correlation coefficients between the parental order of dominance (Wr+Vr) and the parental measure (Yr) for harvests 1 and 2 give a reliable estimate that recessive genes are mostly positive in effect, increasing susceptibility to cuticle cracking. This estimate is only a trend for harvest 3. Narrow sense and broad sense heritability were moderate to high and increased with each harvest.

'C-28' and 'FM-9' appeared to express more dominant than recessive alleles over all harvests. Fla. 7497 expressed more dominant than recessive alleles at harvests 1 and 2, but more recessive than dominant alleles at harvest 3. Under low and very high environmental stress 'Suncoast' expressed more dominant than recessive alleles. Under moderate stress the same cultigen expressed more recessive alleles. Cultigen Fla. 7181 expressed more recessive than dominant alleles at all harvests.

Griffing's Method 2 (using pooled reciprocals), Model 1 (chosen parents, limited number) was used for data analysis. General combining ability (GCA) was significant at all harvests, whereas specific combining ability (SCA) was significant at only harvest 3 (Table 4-9).

Table 4-9. Griffing's analysis for incidence of cuticle cracking, Spring 1994 full diallel.

Harvest 1

Source	df	MS	F
GCA	4	0.004	26.345*[z]
SCA	10	0.0002	1.547
Error	42	0.0001	

Harvest 2

Source	df	MS	F
GCA	4	0.024	32.016*
SCA	10	0.001	1.270
Error	42	0.0007	

Harvest 3

Source	df	MS	F
GCA	4	0.023	54.384*
SCA	10	0.0021	4.981*
Error	28	0.0004	

[z] An * indicates significance at $p \leq 0.05$

Spring 1995 half diallel. Harvest and cultigen effects were significant for the incidence, severity, and index of cuticle cracking (CC) with a significant harvest by cultigen interaction for incidence and index (Table 4-10). For each measure of CC, harvest 2 was greater than harvest 1. Subsequently, all further analyses were conducted on a by harvest basis. Severity of cuticle cracking did not differ enough between parents to make it useful for this genetic study, and cuticle cracking index did not provide any information different from incidence; therefore, incidence of cuticle cracking was the focus of this analysis.

On an individual harvest basis less distinction in incidence of CC between the parents occurred than in 1994. At harvest 1, the incidence of CC was highest for 'Suncoast', but it was not significantly different from Fla. 7181 (Table 4-11). Fla. 7181 had higher incidence than 'C-28', but it was not significantly different from 'FM-9' and Fla. 7497. 'C-28' had the lowest incidence, but this was not significantly different from Fla. 7497 and 'FM-9'. Due to high variances in all cultigens, F_1 hybrids were not significantly different from one or both parents. Six of 10 hybrids had incidences of CC intermediate to the parents and less than the MP (Table 4-12a). Hybrids greater than the MP had either 'C-28', Fla. 7181, or both as a parent. Two RxS hybrids were not significantly different from the susceptible parent, each with 'C-28' as the resistant parent. One RxS hybrid ('FM-9' x 'Suncoast') was not significantly different from the resistant parent. All RxR and SxS hybrids were intermediate to the parents and less than the MP.

Fla. 7181 had a significantly higher incidence of CC at harvest 2 than all other parents (Table 4-11). Incidence of CC for 'Suncoast', Fla. 7497, and 'FM-9' were not significantly different. 'C-28' had the lowest incidence, but it was not significantly different from that of 'FM-9'.

Table 4-10. Analysis of variance for parental and F_1 cultigens in 1995.

INCIDENCE[z]

Source	df	MS	P value
Block	3	0.01	0.54
Cultigen	14	0.20	<0.001
Error a	42	0.03	
Harvest	1	1.95	<0.001
Harvest*Cultigen	14	0.02	0.03
Error b	3	0.06	
Total	77		

SEVERITY[y]

Source	df	MS	P value
Block	3	0.53	0.03
Cultigen	14	0.35	0.03
Error a	40	0.19	
Harvest	1	5.50	<0.001
Harvest*Cultigen	13	0.27	0.11
Error b	3	0.62	
Total	74		

INDEX[x]

Source	df	MS	P value
Block	3	0.04	0.37
Cultigen	14	0.84	<0.001
Error a	42	0.10	
Harvest	1	14.76	<0.001
Harvest*Cultigen	14	0.22	<0.001
Error b	3	0.26	
Total	77	0.05	

[z] %Fruit affected
[y] Mean for all affected fruit
[x] Severity mean for all fruit

Table 4-11. Incidence of cuticle cracking for parents (1995).

Cultigen	Harvest 1	Harvest 2
Fla. 7181	7.8ab[z]	55.7a
Suncoast	18.7a	34.9b
Fla. 7497	3.2bc	26.1b
FM-9	8.8bc	15.4bc
C-28	0.4c	7.0c

[z] Mean separation within columns by Duncan's multiple range test at $p \leq 0.05$

At harvest 2, incidences of CC for 2 of 6 RxS F_1 hybrids were not significantly different from the susceptible parent, both having 'C-28' as the resistant parent. One RxS hybrid ('FM-9' x 'Suncoast') was not significantly different from the resistant parent. Two of 3 RxR hybrids were not significantly different from the more resistant parent. The SxS hybrid was intermediate to the parents and less than the MP.

Results of the Hayman's analysis are in Table 4-13. Data from block 1 of harvest 1 were significantly different from other blocks and rendered the analysis invalid due to non-uniformity of Wr-Vr. Therefore, those data were not included in the harvest 1 analysis. Variation due to additive gene effects (d) was significant for all harvests. Dominance effects (h^2) over all heterozygous loci in all crosses remained the same for each harvest, but were significant only at harvest 2. Means of the progeny minus

parental means ($m_{L1} - m_{L0}$), indicating direction and degree of dominance, were negative and increased in degree from harvest 1 to harvest 2.

Table 4-12. Incidence of cuticle cracking for F_1 hybrids (1995).

a. Harvest 1

Male / Female	C-28	FM-9	Fla. 7497	Suncoast	Fla. 7181
C-28	-	0.6	0.1	14.0[zx]	16.2[zx]
FM-9		-	0.0[w]	0.3[y]	3.3
Fla. 7497			-	7.7	7.1[z]
Suncoast				-	7.8
Fla. 7181					-

b. Harvest 2

Male / Female	C-28	FM-9	Fla. 7497	Suncoast	Fla. 7181
C-28	-	14.0[z]	1.7[y]	23.4[zx]	50.3[zx]
FM-9		-	3.3[y]	10.3[y]	21.5
Fla. 7497			-	15.8	36.2
Suncoast				-	40.3
Fla. 7181					-

[z] > Mid-parent
[y] Not significantly different from more resistant parent (Table 4-11)
[x] Not significantly different from more susceptible parent
[w] Significantly less than both parents (overdominance)

Table 4-13. Hayman's analysis for incidence of cuticle cracking, Spring 1995 half diallel.

Parameter	Harvest 1	Harvest 2
d^z	0.0033*[t]	0.0090*
h^{2y}	-0.0027	0.0026*
$m_{1-4} - m_{5-8}$[x]	-0.0100	-0.0154
$(H_1/d)^{0.5w}$	0.9079	1.3977
h^2/H_2[v]	0	1
r for Wr+Vr and Yr[u]	0.283	-0.284
NS heritability	0.45	0.48
BS heritability	0.62	0.68
'C-28'	R[s]	R
'FM-9'	D	D
Fla. 7497	D	R
'Suncoast'	R	R
Fla. 7181	D	D

[z] Additive gene effects
[y] Dominance gene effects
[x] Degree and direction of dominance
[w] Dominance type (>1=over-dominance, <1=partial dominance)
[v] Number of gene groups exhibiting dominance
[u] Correlation coefficient between parental order of dominance and parental measure (indicates reliability of gene effect estimates)
[t] An * indicates significance at $p \leq 0.05$
[s] Type of alleles more frequent: D=dominant R=recessive

Likewise, the degree of dominance $[(H_1/d)^{0.5}]$ increased from harvest 1 to harvest 2. The number of gene groups exhibiting dominance, as indicated by h^2/H_2, were 0 and 1 for harvests 1 and 2, respectively. The correlation coefficients between the parental order of dominance (Wr+Vr) and the parental measure of incidence (Yr) indicated that an equal or varying proportion of dominant genes are positive or negative in effect, equally increasing or decreasing resistance to CC. A reversal in direction of r indicates that gene effects reversed from harvest 1 to harvest 2.

Recessive genes increased incidence of CC at harvest 1 and decreased CC at harvest 2. The low correlation coefficient (r) indicates that selection for resistance to CC under the tested conditions would be moderately successful (Hayman, 1954).

Narrow sense heritability increased slightly from harvest 1 to harvest 2, as did the broad sense heritability. 'FM-9' and Fla. 7181 expressed more dominant than recessive alleles for both harvests. 'C-28' and 'Suncoast' expressed more recessive alleles than dominant. Fla. 7497 switched from expressing more dominant alleles to more recessive alleles from harvest 1 to harvest 2.

Griffing's Method 2, Model 1 was used for data analysis. General combining ability (GCA) and specific combining ability (SCA) were significant for both harvests (Table 4-14), with GCA being larger than SCA for both harvests.

Discussion

Consideration of reciprocal differences between hybrids is important to maximize hybrid resistance to cuticle cracking. In this study it was found that significant reciprocal differences in incidence and index of cuticle cracking occurred for one ('C-28' x Fla. 7181) out of 6

Table 4-14. Griffing's analysis for incidence of cuticle cracking, Spring 1995 half diallel.

Harvest 1

Source	df	MS	F
GCA	4	0.003	8.18*[z]
SCA	10	0.002	4.11*
Error	28	0.0004	

Harvest 2

Source	df	MS	F
GCA	4	0.024	18.25*
SCA	10	0.003	2.17*
Error	42	0.001	

[z] An * indicates significance at $p \leq 0.05$

resistant by susceptible crosses only at harvest 3 in 1994. The incidence and index of cuticle cracking was greater in the hybrid with the more susceptible parent as the female than the reciprocal. Reciprocal differences do not appear to be highly significant for crosses between parents having a wide range of incidences, but under moderate environmental stress conditions, using the more resistant parent as female could improve the likelihood of increasing resistance in F_1 hybrids.

Incidence of cuticle cracking shows a better distinction between resistant and susceptible lines than index or severity of cuticle cracking over all environmental conditions tested. These data are easiest to collect and incidence is recommended as the measure of resistance to cuticle cracking for selection purposes.

Results of the analyses over two years are in partial agreement. All genetic effects were controlled by additive or dominant gene action with no epistasis detected. Additive gene effects were of more importance than dominance, though dominance in the direction of lower incidence of cuticle cracking becomes significant under high environmental stress. Dominance in the direction of resistance to incidence of CC was expressed as partial dominance to overdominance. The latter was due to cuticle cracking incidence less than the more resistant parent in some F_1s derived from resistant by resistant crosses.

Resistant by susceptible crosses in 1994 expressed dominance in the direction of resistance to CC as partial to complete dominance, whereas in 1995 the direction and degree of dominance was variable. Radial cracking of peppers (Johnson and Knavel, 1990) has been reported to be under control of dominance effects in the form of overdominance. One gene group expressing dominance is indicated as being associated with cuticle cracking resistance under moderate to high stress.

Broad sense and narrow sense heritability increase with environmental stress and ranged from 0.54 to 0.69 and from 0.67 to 0.89, respectively, in 1994. The degree of dominance increased to a slightly greater extent from 1994H2 to 1994H3 than did BS heritability. This may be due to the findings that at 1994H2 dominant alleles reduced the incidence of CC, whereas at 1994H3 reduction of incidence of CC by dominant alleles was only a trend, with some dominant alleles increasing incidence, thereby reducing the predictability (heritability) of the F_1s. For best results select for resistance to cuticle cracking under moderate environmental stress conditions, if possible, in order to maximize additive gene effects and expression of dominant alleles reducing cuticle cracking.

The 1994 full diallel analysis indicated that resistance is dominant to susceptibility, which was expressed as the majority of reciprocal hybrids having

incidences of CC less than the MP at each harvest. The 1995 half diallel indicated that equal or varying numbers of dominant genes increase or decrease resistance. Dominance of resistance over susceptibility is in contrast to the genetic control of radial cracking in tomatoes (Reynard, 1951), in which resistance appears to be recessive to susceptibility.

Results from the two years differ in the performance of individual parental lines. 'C-28' and Fla. 7181 seemed to reverse in the type of alleles being expressed. This could be the result of a major difference of the F_1 hybrids from the cross. In 1995 the 'C-28' x Fla. 7181 hybrid performed more like its reciprocal from the year before. This reciprocal (Fla. 7181 x 'C-28') was significantly higher in incidence than the 'C-28' x Fla. 7181 hybrid. Attempts to resolve the difficulty with this cross have to be done in the future.

Significant general combining ability coupled with moderate heritabilities for our population suggest that progress can be made in resistance to cuticle cracking at the F_1 hybrid level. However, predicting the performance of specific F_1 lines may be difficult due to significant SCA and dominance effects. Significant overdominance in the Fla. 7497 x 'FM-9' and Fla. 7497 x 'C-28' crosses indicates that progress is possible even in crosses between resistant parents. The results of those crosses also suggest that the

parents are under different genetic control for resistance. Each parent has at least one trait that is complemented by the other, resulting in reciprocal hybrids that are significantly more resistant to cuticle cracking than either parent. Due to differences in expression of dominant and recessive alleles in 1995, resistance to cuticle cracking in 'C-28' and 'FM-9' also appear to be under different genetic control. Transgressive segregation for resistance to cuticle cracking in hybrids from a cross between 'C-28' and 'FM-9' should be possible.

CHAPTER 5
ANATOMICAL CHARACTERISTICS OF TOMATO RELATED TO CUTICLE CRACKING

Introduction

Cuticle cracking (rain check) is a disorder occurring primarily in mature-sized tomato fruit (*Lycopersicon esculentum*, Mill.) causing degradation of appearance and shelf-life (Young, 1947). This disorder is characterized by hair-like cracks in the cuticle covering all or a portion of the calyx end, and may extend down the sides of the fruit (Hayman, 1987; Young, 1947). In more severe form cuticle cracks may penetrate to the epidermal wall to form lenticel-like lesions characterized by suberin production (Faust and Shear, 1972; Tukey, 1959). Occurrence of this disorder is predominately two to three weeks prior to breaker stage, when the fruit are rapidly expanding (den Outer and van Veenendaal, 1987).

Fruit epicarp anatomy and morphology. The pericarp of tomato fruit is covered and protected by several layers of cells and waxy cuticle collectively referred to as the epidermis or 'skin'. These layers include epidermal cell layers, underlying hypodermis composed of collenchyma, and

overlying cutinized layers (cuticle) (Groth, 1910). The cell wall of the outer epidermal layer and overlying cutinized regions are highly integrated in tomato fruit (Holloway, 1980; Wilson and Sterling, 1976), and will be referred to as the epicarp (Wilson and Sterling, 1976). Epidermal strength and elasticity may be involved with susceptibility to cuticle cracking. The epidermal layer must be strong enough to resist cracking during expansion but must also be elastic to allow for expansion (Voisey et al., 1970). Controversy exists concerning the role of the epicarp in resistance to cuticle cracking. den Outer and van Veenendaal (1987) found that tomato fruits that showed cuticle cracking had an epicarp near carpel walls up to 80% thicker than fruits without cracking. The cracks were found to occur first in the cuticle over carpel walls. They suggested that the thickness of the epicarp may have reduced the elasticity of the epidermis and made it more susceptible to cracking under pressure. Varieties of tomato susceptible to radial cracking have been shown to have low epidermal extensibility and an average or low tensile strength (Kamimura et al., 1972). Those reports are in contrast with a study by Borowiak and Habdas (1988), which found that tomato fruits from varieties resistant to mechanical injury had thick cuticle layers as compared to more susceptible varieties.

The shape of epidermal cells has been found to correlate with susceptibility to radial cracking. An early study by Heddins (1964) described rupture resistant tomato fruit as having extensive cutin and small, flattened, thick-walled parenchyma beneath the epidermis. Later studies identified radial cracking resistant fruit as having flattened and presumably tougher epidermal cells (Cotner et al., 1969; Hankinson and Rao, 1979), as compared to susceptible lines showing rounded epidermal cells (Hankinson and Rao, 1979).

Calcium nutrition has been shown to be involved with epidermal cracking in tomatoes, apples, and cherries (Dickinson and McCollum, 1964). Calcium is important in the production of rigid cell walls (Dey and Brinson, 1984) and middle lamella as calcium pectinate. When applied to the surface of cherry and tomato fruits, calcium can reduce cracking by strengthening the cell walls (Dickinson and McCollum, 1964; Glenn and Poovaiah, 1989; Jensen et al., 1960). Cracking of tomato epidermis has been shown to occur under pressure by the separation of cell walls rather than cell disruption (Hankinson and Rao, 1979) possibly due to lack, or uneven distribution of calcium pectinate. Ehret (personal communication, 1995) has determined by light microscopy that cuticle cracks originate over cell junctions. It was suggested that a weakness in the middle lamellae at those junctions may allow the epidermal cells to

shift in position and place stress on the cuticle. Cuticular splitting could result in releasing enough turgor pressure to prevent epidermal rupture (concentric cracking).

Cuticle thickness is a factor in the russeting of apples, cracking of tomatoes, and susceptibility of tomato fruits to mechanical injury. Apple varieties with thinner or less regular cuticles are more susceptible to russeting (Faust and Shear, 1972). Tomato fruits with thick cuticle layers are less susceptible to radial and concentric cracking (Voisey et al., 1970) and mechanical injury (Borowiak and Habdas, 1988). Thinness or unevenness of the cuticle has been implicated as a possible weakness, at which point cracking could be caused by tangential division of epidermal cells exerting pressure on the cuticle (Brown and Considine, 1982; Meyer, 1944). It has been suggested that sun exposure may change the polymerization of cuticular waxes of apples making the fruit more susceptible to cracking (Vries, 1970).

Fruit anatomy and morphology. Fruit shape and size may affect susceptibility to cuticle cracking. The theoretical role of fruit shape and distribution of stress has been investigated by Considine and Brown (1981). Their studies, based on models of axisymmetric fruit shapes, indicate that stresses should be uniform for globe shaped fruit, whereas stress due to internal pressure is focussed at the upper region or shoulder of flat round (oblate spheroid) fruit,

making them more susceptible to cracking. Genetic studies with peppers (Johnson and Knavel, 1990) indicate that fruit shape is less important in determining crack resistance than properties of the cuticle and/or epidermis. Some studies indicated that large tomato fruit were more susceptible to cuticle cracking (Considine and Brown, 1981; Janse, 1985; Koske et al., 1980), whereas others showed them to be either less susceptible (Bakker, 1988) or that size was not a factor involved in cuticle cracking (Ehret et al., 1993). Cotner et al. (1969) found that resistant lines also displayed increased and deeper vascularization in fruit with few locules as compared to susceptible fruit with little vascularization and many locules. Thus, the resistant lines were better able to distribute absorbed water and reduce pressure on the epidermis than the more susceptible lines.

Water allocation and distribution to and from fruit may be affected by the anatomy of the pedicel. Jointed pedicels form an abscission zone, thereby restricting the flow of water into or out of the fruit. In comparison, jointless pedicels do not form an abscission zone, creating a situation in which water potentially could enter the fruit more freely during the last stages of maturation when cuticle cracking is most prevalent.

The objectives of this study were to 1) describe the ultrastructure of tomato fruit epicarp as related to cuticle cracking and 2) investigate the relationship between epicarp and whole fruit anatomy (pedicel) and morphology (size, shape, and light reflectance), and incidence and severity of cuticle cracking.

Materials and Methods

Epicarp anatomy and morphology. Epicarp ultrastructure of tomato fruit as related to cuticle cracking was described using electron and light microscopy. Electron and light microscopy, and light reflectance measures of both resistant and sensitive cultigens (cultivars, varieties, and breeding lines) (Soule, 1985), as well as their F_1 and F_2 hybrids, were employed to determine if there were any differences in the epicarp which may be related to incidence or severity of cuticle cracking (CC).

1994 samples. Cultigens Fla. 7181 and 'Suncoast' (Scott et al., 1985) were selected as susceptible cultigens, whereas Fla. 7497, 'FM-9' (Leeper and Cox, 1986), and 'C-28' (Moore, 1971) were chosen as resistant cultigens. Each cultigen (Appendix B-3A) was seeded in the greenhouse in Black Beauty spent coal (Reed Minerals Div., Highland, IN)

medium on 24 January and transplanted into Todd planter flats (3.8-cm^3 cell size) (Speedling, Sun City, FL) containing a 1:1 peat and vermiculite mixture on 7 February. Plants were set into the field at the Gulf Coast Research and Education Center, Bradenton, Fla. on 8 March in a randomized, complete-block design. Cultigens not used in this study were included in the field. Each of 4 blocks had 30 plots containing 8 plants of an individual parental or F_1 hybrid line. Plots were randomly arranged in 6 rows per block. Mature-green and riper fruit were harvested three times, at weekly intervals, from all plants per plot. Fruit for this study were chosen from the third harvest (1994H3). Twenty fruit, 10 with CC and 10 without CC, were selected for each cultigen. Light reflectance readings were taken for each fruit prior to preparation for transmission electron microscopy (TEM). Severity of CC for affected fruit was determined on a scale from 1 to 10, based on the percentage of surface area covered with visible cuticular cracks (Appendix A).

1995 samples. Cultigens Fla. 7181 and 'C-28' (Moore, 1971) were selected as parents from which F_1 and F_2 generations were produced. Each cultigen from the above family (Appendices B-3 and B-4A) was seeded in the greenhouse in Black Beauty spent coal (Reed Minerals Div., Highland, IN) medium on 23 January and transplanted into Todd planter flats (3.8-cm^3 cell size) (Speedling, Sun City,

FL) containing a 1:1 peat and vermiculite mixture on 8 February. Plants were set into the field at the Gulf Coast Research and Education Center, Bradenton, Fla. on 8 March in a randomized, complete-block design. Cultigens not used in this study were included in the field. Each of 4 blocks had 15 eight-plant plots, each with an individual cultigen. Plots were randomly arranged in 6 rows per block. Mature-green and riper fruits were harvested two times, at a two week interval, on an individual plant basis. Samples for this study were selected from the second harvest (1995H2). One to 3 fruit without CC were selected from each parent and the F_1 hybrid for transmission electron microscopic (TEM) analysis. Fruit from five F_2 plants, ranging from 0 to 96.3% incidence, were sampled. One to 3 fruit without CC from each of the F_2 plants were selected for TEM analysis.

TEM sample fixation. Epidermal sections from fruit shoulder regions were immersed in 2% glutaraldehyde buffered at pH 7.2 in 0.1M sodium cacodylate buffer for 2 hours. Sections were washed twice at 15 minutes each with 0.1M cacodylate buffer followed by overnight immersion in 1% osmium tetroxide in 0.1M sodium cacodylate buffer. Samples were then washed for 10 minutes with 0.1M sodium cacodylate buffer followed by two 10 minute rinses in distilled water (Dykstra, 1993). All fixation steps took place at 4°C.

Dehydration. Fixed samples were dehydrated through an ethanol/acetone series at 4°C as follows: 10 minute

immersions in 25, 50, 75, and 100% ethanol; two 1 hour immersions in 100% ethanol; three 10 minute washes in 100% acetone.

Embedding. Dehydrated samples were embedded with Spurr's resin (1969) by immersion in 30% resin in acetone for 3 hours. This was followed by a 3 hour immersion in 70% resin and 3 hours in 100% resin. The samples were held overnight in fresh 100% resin and then transferred to a change of 100% resin and hardened in a 60°C oven overnight.

Post-staining of thin sections on grids. Embedded samples were mounted on plastic or aluminum stubs and thin sectioned on an LKB Nova Ultramicrotome. Sections were placed on 75 mesh copper grids and post-stained. Polysaccharides were stained with 1% barium permanganate (Hoch, 1977) for 30 seconds, followed by a distilled water rinse. This was followed by a 15 minute staining with 5% uranyl acetate, distilled water rinse, a 3 to 4 minute stain with Reynolds' (1963) lead citrate, and a final distilled water rinse.

Measurements. Sections from one fruit with CC and one fruit without CC from each cultigen in 1994, and 1 to 3 fruit without CC in 1995, were viewed and photographed with a Zeiss EM-10CA transmission electron microscope. Measurements were taken of epidermal cell length and depth and the thickness of the epicarp (Figure 5-1). Five to 18 cells from fruit with cuticle cracking and 9-27 cells from

fruit without cuticle cracking were measured per cultigen in 1994. Six to 32 cells from fruit without CC were measured per cultigen in 1995. Extensive integration of the waxy cuticle and cell wall made it impossible to distinguish a boundary between the two, and thus to make separate measurements. A log transformation was used on epidermal cell measurement to make variances independent of the means. Data were analyzed by PROC GLM and PROC CORR procedures of the Statistical Analysis System (SAS Institute, 1979).

Scanning electron microscopy sections. Epidermal peels from fruit with and without CC were air dried in the presence of a desiccant and mounted on aluminum specimen stubs using double faced tape. The appearance of cuticular waxes was viewed and photographed using a Hitachi S-4000 scanning electron microscope.

Epidermal reflectance. Light reflectance (L) of fruit with and without cuticle cracking was measured at 3 positions (shoulder, middle, and blossom end) per fruit with a HunterLab spectrocolorimeter (Hunter, 1975) and averaged for analysis. Ten fruit, 5 with cuticle cracking and 5 without, were measured for each of the following cultigens: 'C-28', 'FM-9', Fla. 7497, 'Suncoast', and Fla. 7181. Light reflectance values were correlated with epidermal and cuticular morphology and incidence and severity of cuticle

cracking using the PROC CORR procedure of the Statistical Analysis System (SAS Institute, 1979).

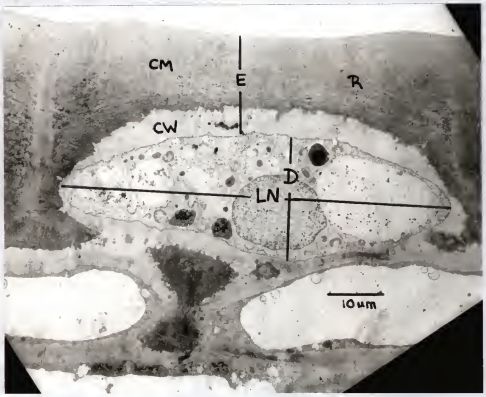


Figure 5-1. Transverse section of epidermal and cuticular layers of tomato fruit cultigen 'FM-9' x 4230. The cuticular membrane (CM) is approximately 15 um in thickness with a reticulate (R) ultrastructure throughout, showing no distinct boundary with the cell wall (CW). Cell length (LN), depth (D), and epicarp (E) were measured (um) for selected cultigens.

Fruit anatomy and morphology. Parental lines, F_1 hybrids, F_2, backcross to resistant parent (BC_1), and backcross to susceptible parent (BC_2) generations were grown for two families ('C-28' x 'Suncoast' and Fla. 7497 x Fla. 7181) (Appendices B-3 and B-4). 'Suncoast' and Fla. 7497 have globe shaped fruit (Appendix D) and differ in resistance to cuticle cracking (CC) (Table 5-1). Fla. 7497 has an arthritic type pedicel in which the pedicel is swollen above the abscission zone and does not separate cleanly from it. Fla. 7181 has flat-round fruit and jointless pedicels (Appendix D). 'C-28' has flat-round fruit and jointed pedicels. Two near-isogenic lines (NIL) (Fla. 7547 and Fla. 7481) (Scott and Jones, 1995) differing by pedicel anatomy were included. Cultigens were seeded in the greenhouse in Black Beauty spent coal (Reed Minerals Div., Highland, IN) medium on 23 January and transplanted into Todd planter flats (3.8-cm^3 cell size) (Speedling, Sun City, FL) containing a 1:1 peat and vermiculite mixture on 8 February. Plants were set into the field at the Gulf Coast Research and Education Center, Bradenton, Fla. on 8 March in a randomized, complete-block design. Each of 4 blocks had 36 plots, each containing 8 plants of an individual cultigen. Parental and F_1 lines had one plot per block, backcross lines had 4, and F_2 lines had 6. Plots were randomly arranged in 6 rows per block. Mature-green and riper fruits were harvested two times at a two week

interval, on an individual plant basis. Fruit from the second harvest (1995H2) were used for this study. Incidence and severity of cuticle cracking and individual fruit weight (size) were determined for each cultigen. Incidence and severity data were transformed using the square root function to make the variances homogeneous (Zar, 1984). Data were analyzed by the PROC GLM, PROC TTEST, and PROC CORR procedures of the Statistical Analysis System (SAS Institute, 1979). Means were compared by Duncan's multiple range test using PROC GLM (SAS Institute, 1979). All analyses were conducted on plants with a minimum of ten fruit at 1995H2.

Table 5-1. Cultigens used in testing effects of fruit shape and pedicel anatomy on incidence and severity of cuticle cracking.

Cultigen	Shape[z]	Pedicel[y]
C-28	F	j_o
Suncoast	G	j_o
Fla. 7497	G	j_a
Fla. 7181	F	j_2
Fla. 7547	F	j_o
Fla. 7481	F	j_2

[z] F=Flat-round, G=Globe
[y] j_o=jointed, j_2=jointless, j_a=arthritic joint

Results

Description of epicarp anatomy and morphology. The cell wall and cuticle of tomato fruit are not separated at a distinct boundary, but are highly integrated (Figure 5-2). Cutin uniformly covers the epidermal surface of the fruit, permeates the cell wall, and extends between the initial layer of epidermal cells into the hypodermis (Figs. 5-2 and 5-3). The reticulate material of the cuticle appears to be produced in discontinuous layers above the epidermal wall, separated at cell junctions by non-reticulate, or amorphous, material (Figure 5-2).

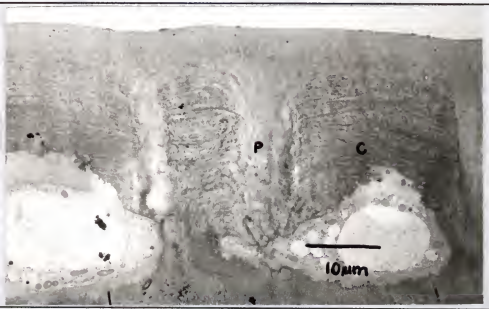


Figure 5-2. Transverse section (TEM) of mature tomato cuticle X 3250. Cutinized layers (C) appear as discontinuous layers of reticulate wax above epidermal cells. The layers end at cell junctions, separated by an amorphous material in the form of 'pegs' (P).

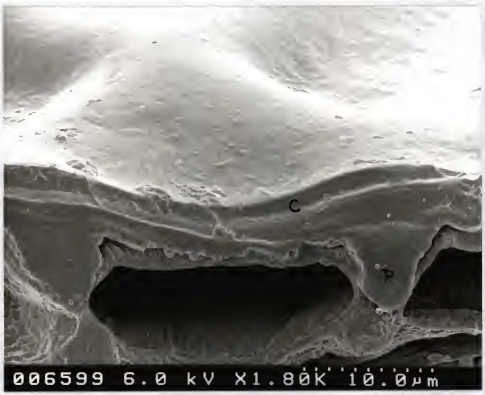


Figure 5-3. Side view (SEM) of mature tomato cuticle X 1800. The cuticle (C) appears as a smooth, continuous material covering the epidermal layer of cells and forming 'pegs' (P) at cell junctions.

From the observation of 17 cuticle cracks 1.0-2.0 mm in length, 82% originated over cell junctions, 12% above the cytoplasm near a cell junction, and 6% originated at the middle of a cell. All cuticle cracks were perpendicular to the direction of elongation of the outer epidermal layer.

Short cracks appeared as shallow splits in the cuticle. Long cracks extended deeper through the cuticle to the epidermal cell (Figure 5-4).

Figure 5-4. Surface view (SEM) of mature tomato cuticle X 400 with cuticle cracking.

Anatomical relationship to cuticle cracking. Significant cultigen differences were found for all measures of the epidermal and cuticular layer of tomato fruits in both years (Tables 5-2 and 5-4). For 1994 resistant cultigens 'C-28', 'FM-9', and Fla. 7497 had epicarp thicknesses (E) greater than 10um (Table 5-3). This was significantly greater than for susceptible cultigens 'Suncoast' and Fla. 7181. The ratio of epicarp thickness to cell depth (E/D) for resistant cultigens was greater than 1.25, and significantly different from the ratio for susceptible cultigens, which were all less than 1.00 (Table 5-3). Thickness of the epidermal cell cytoplasm plus the epicarp (D+E) was significantly greater for cultigen 'C-28' than all other cultigens. This was followed by Fla. 7497, which was significantly greater than 'FM-9' and Fla. 7181, which in turn were significantly greater than 'Suncoast'. In 1995 all epicarp and epidermal measures for 'C-28' were significantly greater than those for Fla. 7181 (Table 5-4). Measures for F_1 and F_2 fruit fell between those of the two parents.

Significant severity differences were found for epicarp thickness (E) and thickness of the epidermal cell cytoplasm plus epicarp (D+E) (Table 5-2). Fruit with a CC severity of 6 had significantly thinner E and D+E measures than fruit with lower severity levels (Table 5-3). Significant cultigen-by-severity interaction effects on D+E and E were found (Table 5-2).

Table 5-2. Analysis of variance for epidermal and cuticle measurements (1994).

Source	df	MS	P value
Cell Shape			
Cultigen	4	6.71	<0.001
Severity	4	8.38	<0.001
Cultigen*Severity	1	3.16	0.04
Error	113	0.74	
Total	122		
Occurrence[z]	56.1		<0.001
Cell Depth Plus Epicarp			
Cultigen	4	0.08	<0.001
Severity	4	0.04	<0.001
Cultigen*Severity	1	0.06	<0.001
Error	128	0.002	
Total	137		
Ratio of Epicarp to Cell Depth			
Cultigen	4	2.64	<0.001
Severity	4	0.51	0.42
Cultigen*Severity	1	0.02	0.85
Error	128	0.52	
Total	137		
Thickness of Epicarp			
Cultigen	4	0.28	<0.001
Severity	4	0.08	<0.001
Cultigen*Severity	1	0.06	0.01
Error	128	0.01	
Total	137		

[z] Analyzed by Student's t-Test as presence or absence of cuticle cracking

Table 5-3. Measurements of cuticle and epidermis (1994)[v].

	Shape[z]	D+E[y]	E/D[x]	E[w]
Cultigen				
C-28	2.17c	23.48a	1.28a	11.37a
FM-9	3.20a	19.03c	1.30a	10.38a
Fla. 7497	2.98b	21.56b	1.27a	11.37a
Suncoast	2.81b	17.46d	0.64b	6.45c
Fla. 7181	2.78b	19.05c	0.73b	7.76b
Severity				
0	2.7c	20.2a	1.0a	8.7b
3	3.8b	18.1b	1.5a	8.2b
4	3.6b	20.9a	1.2a	11.0a
5	3.5b	19.4ab	1.0a	9.3ab
6	5.0a	14.4c	0.9a	6.5c
C-28				
With CC	3.1a	18.1b	1.5a	8.2b
Without CC	2.2b	24.4a	1.2a	11.6a
FM-9				
With CC	4.2a	17.5a	1.4a	9.3a
Without CC	3.4b	19.5a	1.2a	10.5a
Fla. 7497				
With CC	3.2a	22.9a	1.2a	11.9a
Without CC	2.8a	18.5b	1.4a	9.7b
Suncoast				
With CC	5.0a	14.4b	0.9a	6.5a
Without CC	2.8b	18.1a	0.6b	6.3a
Fla. 7181				
With CC	3.5a	19.4a	1.0a	9.3a
Without CC	2.8b	18.6a	0.5a	6.4a

[z] Ratio of cell length to depth
[y] Cell depth plus epicarp thickness (um)
[x] Ratio of epicarp thickness to cell depth
[w] Epicarp thickness (um)
[v] Mean separation within columns by Duncan's multiple range test at $p \leq 0.05$

Table 5-4. Measurements of cuticle and epidermis (1995)[u].

Cultigen	INCD[z]	Shape[y]	D+E[x]	E/D[w]	E[v]
C-28	7.2	2.50cd	25.48a	1.66a	15.52a
Fla. 7181	57.6	3.08a-c	18.07d	0.95b	8.75d
F_1	50.3	3.64a	18.74d	1.44a	10.72c
F_2	0.0	3.30a-c	22.70bc	1.50a	13.00b
	8.7	3.54ab	23.20b	1.44a	13.19b
	33.3	2.03d	24.72ab	0.92b	11.54c
	84.2	2.79bc	23.25b	1.51a	13.35b
	96.3	3.40ab	20.78c	1.34a	11.54c

[z] Incidence of cuticle cracking
[y] Ratio of length to cell depth
[x] Cell plus epicarp thickness (um)
[w] Ratio of epicarp thickness to cell depth
[v] Epicarp thickness (um)
[u] Mean separation within columns by Duncan's multiple range test at $p \leq 0.05$

Within each cultigen only 2 levels of severity were tested: no CC (0) versus CC at one severity level (1-10). The presence or absence of CC on individual fruit were compared and this is referred to as 'occurrence'. Significant occurrence effects ($p \leq 0.05$) on E were found for cultigens 'C-28' and Fla. 7497, but not for Fla. 7181, 'FM-9', or 'Suncoast' (Table 5-3). No consistent pattern of difference between fruit with CC and fruit with-out CC was found. Significant occurrence effects on D+E were found for cultigens 'C-28', Fla. 7497, and 'Suncoast', but not for 'FM-9' and Fla. 7181. No consistent pattern of difference between fruit with CC and fruit without CC was found. The ratio of epicarp thickness to cell depth (E/D) was significantly higher for fruit with CC than for fruit

without CC for susceptible cultigens Fla. 7181 and 'Suncoast' (Table 5-3).

Incidence of cuticle cracking, in terms of percent fruit affected, was not significantly correlated with any of the thickness measures for 1995 (data not shown). The trend for the parents and F_1 hybrids was for incidence to increase as thickness of E or D+E decreased. This pattern was not evident for the plants sampled in the F_2 generation. It should be noted that susceptible cultigens produce a fair number of 'escape' plants on which fruit are not affected by cuticle cracking. Progeny tests are needed to determine if the F_2 cultigens with low incidences are resistant or 'escape' susceptibles.

Fruit with the greatest severity of CC had significantly greater length to depth ratios of epidermal cells than fruit at all other severity levels (Table 5-3). Severity increased with increasing length to depth ratio of epidermal cells. Cell shape in fruit with CC was significantly different from those without CC for all cultigens except Fla. 7497 (Table 5-3). Fruit with CC had a greater length to depth ratio.

Cultigen differences and severity of cuticle cracking significantly affected light reflectance (L) of the fruit (Table 5-5). All cultigens were significantly different from each other (Table 5-6), with more resistant cultigens having lower L values than susceptible cultigens.

Table 5-5. Analysis of variance for light reflectance (L) of tomato fruits (1994).

Source	df	MS	P value
Cultigen	4	18.26	<0.001
Severity	4	225.94	<0.001
Cultigen*Severity	1	759.87	<0.001
Error	128	0.00	
Total	137		
Occurrence[z]	68.5		<0.001

[z] Analyzed by Student's T-Test as presence or absence of cuticle cracking

Table 5-6. Light reflectance (L) of tomato fruits[z].

	L
Cultigen	
C-28	66.18c
FM-9	62.84d
Fla. 7497	60.15e
Suncoast	67.53a
Fla. 7181	66.35b
Severity	
0 (No cracking)	66.33a
3	63.18d
4	59.66e
5	64.98b
6	64.32c
Occurrence	
Fruit not Cracked	66.33
Fruit Cracked	61.78

[z] Mean separation within columns by Duncan's multiple range test at $p \leq 0.05$

Absence of cuticle cracks significantly increased L values over the presence of cracks (Tables 5-5 and 5-6). Light reflectance significantly decreased as severity of CC increased (Table 5-7), although not directly by the severity scale (Table 5-6). A significant cultigen by severity interaction was due to 'FM-9', in which the presence of cracks significantly increased light reflectance (data not shown).

Light reflectance was significantly correlated to measures of the epidermal and cuticular layers of tomato fruit (Table 5-7). As the thickness of the epicarp plus cell depth increased, L decreased, explaining 18.5% (r^2) of the variation in L. Light reflectance decreased significantly as epicarp thickness increased, explaining 5.8% of the variation in L. As the ratio of epicarp to cell depth increased, L decreased, explaining 4% of the variation in L.

Table 5-7. Pearson correlation coefficients (r) and probabilities for epidermal measurements, severity of cuticle cracking, and light reflectance (L).

	L
Severity	-0.50 p<0.001
Thickness of epicarp	-0.43 p<0.001
Cell depth plus epicarp	-0.24 p=0.004
Ratio of epicarp to cell depth	-0.20 p=0.02

Fruit anatomy and morphology. Four segregating generations from resistant by susceptible crosses were tested and a significant difference between incidence of CC in globe fruit versus flat-round fruit was found only for the F_2 generation of the Fla. 7497 x Fla. 7181 cross, where plants producing globe shaped fruit had a significantly greater incidence of CC than plants producing flat-round fruit (Table 5-8). In two 'C-28' x 'Suncoast' generations, (BC to 'Suncoast' and F_2) the trend was for plants producing globe shaped fruit to have higher incidences of CC than plants producing flat-round fruit, whereas in the BC to Fla. 7181 generation from the Fla. 7497 x Fla. 7181 cross, the trend was reversed (Table 5-8).

Table 5-8. Fruit shape effects on incidence of cuticle cracking[z].

Generation	Flat-round	Globe
Fla. 7497 x Fla. 7181		
BC_1	7.1	6.4ns
F_2	15.4b	25.1a
C-28 x Suncoast		
BC_2	10.8	16.9ns
F_2	4.3	6.3ns

[z] Mean separation within rows by Student's t-Test at $p \leq 0.05$. ns indicates not significantly different. Data were transformed to square roots before analysis.

The distribution of plants within incidence categories differed between the two shapes (Table 5-9). Less than 20% of the plants with either shaped fruit had no incidence of cuticle cracking. Fifty-two percent of the plants producing globe shaped fruit had incidences of CC equal to or below 30%, whereas 77% of plants producing flat-round fruit fell into the same category. Eleven percent of the plants producing globe shaped fruit had no CC, indicating that resistant globe shaped fruit are possible to produce.

Table 5-9. Incidence of cuticle cracking in plants producing globe versus flat-round fruit from the F_2 generation of Fla. 7497 x Fla. 7181.

INCIDENCE	GLOBE	FLAT-ROUND
0	11[z]	16
10	14	20
20	19	24
30	8	17
40	11	9
50	14	8
60	6	1
70	8	2
80	3	2
90	3	0
100	3	2

[z] Plants (%) within Incidence category

Incidence of CC significantly increased with fruit size (Table 5-10), with size explaining 33% of the variance in incidence ($r^2 = 0.33$, $p<0.001$). Severity of CC significantly increased with fruit size at 1995H2 (Table 5-10),

with fruit size explaining 17% of the variance in severity ($r^2 = 0.17$, $p<0.001$).

Significant effects of pedicel anatomy on incidence of CC were found only for the F_2 generation of the Fla. 7497 x Fla. 7181 cross (Table 5-11). Plants with jointed pedicels had significantly lower incidences of CC than plants with jointless pedicels. Generations with nonsignificant differences showed the same trend.

Table 5-10. Regression analysis for incidence and severity of cuticle cracking for harvest 2 in 1995.

Parameter	Estimate	T for H0: Parameter=0	Pr > |T|
Incidence			
INTERCEPT	-0.10	-1.51	0.13
FRUIT SIZE	1.84	8.60	<0.001
$r^2 = 0.33$			
Severity			
INTERCEPT	1.60	16.93	<0.001
FRUIT SIZE	1.47	4.95	<0.001
$r^2 = 0.17$			

Table 5-11. Affect of pedicel anatomy on incidence of cuticle cracking[z].

Generation	Jointed	Jointless
Fla. 7497 x Fla. 7181		
F_2	13.8b	25.6a
BC_2	44.1	46.3ns
C-28 x Fla. 7181		
F_2	21.2	25.1ns
Fla. 7547 vs Fla. 7481	19.4	29.6ns

[z] Mean separation within rows by Student's t-Test at $p \leq 0.05$ ns indicates not significantly different

Discussion

Cuticle cracking of tomato fruit occurs as a result of a rapid or uneven increase of turgor pressure placed upon the cuticle and epidermal wall (epicarp) (Janse, 1985; Hayman, 1987; den Outer and van Veenendaal, 1987). The epicarp must be strong enough to resist cracking, while at the same time have sufficient extensibility to allow for expansion. A thick wall and/or cuticular layer would provide strength for resistance to cracking. In this study it was found that the 3 cultigens most resistant to cuticle cracking had significantly thicker epicarp layers than the

two susceptible cultigens. This is in agreement with the findings of Borowiak and Habdas (1988) for cultigens resistant to mechanical injury, but not with the study by den Outer and van Veenendaal (1987), who showed that fruit with cuticle cracking had thicker epicarp layers than fruit without cuticle cracks. The primary differences between den Outer and van Veenendaal's study and the one presented here were 1) the position of the layers that were tested and 2) how the data were analyzed. Our samples were taken primarily from skin above the locules of the fruit, whereas those of the den Outer study were from above the carpel walls. Turgor pressure on the regions above carpel walls would theoretically be greater than those above the locules due to non-uniformity of the surface and underlying layers (Considine and Brown, 1981). If cuticle cracking occurs first at the carpel wall regions of the epidermis as suggested by den Outer and van Veenendaal (1987) then thick walls in that region would reduce extensibility in the face of high turgor pressure. The more uniform surface and underlying layers above locules would be placed under less severe and less rapid changes in turgor pressure during expansion (Considine and Brown, 1981). Thick walls and covering layers of waxy cuticle would provide strength to resist cracking. The study of den Outer and van Veenendaal compared measures between fruit with and without cuticle cracking from the same cultigen. In our study, within each

cultigen, no significant pattern in difference between fruit with cuticle cracking and fruit without cuticle cracking for epicarp measures was found. A limited number of fruit from each cultigen were tested and may have been a significant factor in obtaining clear results. We know that susceptible lines are highly variable in incidence and severity of cuticle cracking, and it is suspected that they are highly variable in factors affecting incidence and severity, including ultrastructure. A study comparing epicarp measures between regions above carpel walls and above locules for fruit with cuticle cracking and without cuticle cracking within resistant and susceptible cultigens is necessary to clarify the discrepancies.

Thickness of the epidermal wall and overlying layers of cutin may be indirectly estimated using light reflectance (L). Increased thickness of epidermal wall plus cuticle layers, as well as increased thickness of epidermal cell depth plus overlying layers, were significantly correlated to decreased light reflectance, though the amount of variation in L explained by those factors was not great. The wax and cellulose of the epidermal and cuticle layers absorb light; thus, as the thickness of those layers increases, the amount of light reflected decreases. Light reflectance (L) (Hunter, 1975) is indicated to be a useful method for selecting for resistance to cuticle cracking when

all other anatomical and physiological factors between cultigens appear to be equal.

Light microscopic observations from our study and those of Ehret (Personal communication, 1995) have shown that the cuticle cracks in tomato fruit originate primarily in the cuticle above cell junctions. The cutinized layer of the fruit epicarp extends inward between adjacent epidermal cells to form 'pegs' (Holloway, 1980; Wilson and Sterling, 1976). In our study these pegs appear to be composed of nonreticulate material which has a lower electron density than the cuticle material covering the tangential surface of the epidermal cells. This difference in appearance may indicate a difference in chemical structure or morphology of the wax at cell junctions. If this material is weaker than the cuticle overlying the epidermal cell, then as turgor pressure is applied from within the fruit, the cell junctions would pose the least resistance to pressure and be the first areas to crack.

Cell length (LN) to depth (D) ratio provides a measure of cell shape. Elongated cells will have a higher LN to D ratio than more rounded cells. This study shows that differences in severity of cuticle cracking and cultigens occur as LN/D changes. The most resistant cultigen tested ('C-28') had LN/D significantly lower than all other cultigens. Fruit without cuticle cracks had significantly lower LN/D than fruit with cuticle cracks. Fruit from

cultigens resistant to cuticle cracking have less elongated epidermal cells than fruit from cultigens susceptible to cuticle cracking. Den Outer and van Veenendaal (1987) found similar results. The more rounded shape potentially distributes pressure more evenly throughout the cell and to the overlying wall and cuticle, reducing the pressure on any one area (Considine and Brown, 1981), thus reducing the potential for cracking.

Considine and Brown (1981) reported that fruit with more symmetrical shape should theoretically be less susceptible to any form of cracking than more asymmetrical fruit due to more even distribution of the forces from turgor pressure on the skin by symmetrical fruit. In our study it was found that plants producing globe shaped fruit tended to have higher incidences of cuticle cracking than plants producing flat-round fruit. However, four generations from 2 families were tested and in only one generation was this trend significant. Either this finding is in direct opposition to the theoretical considerations of Considine and Brown (1981), or the globe shaped fruit in tomato have linked characteristics that overcome the theoretical resistance to cuticle cracking. Plants producing globe shaped fruit did not differ from plants producing flat-round fruit in mean or distribution for fruit size or number of fruit harvested, factors which have been shown to influence incidence of cuticle cracking (See

Chapter 6). Therefore, differences in other factors influencing cuticle cracking, such as epicarp thickness and/or canopy cover should be considered for study. Plants producing globe shaped fruit are more variable in incidence of cuticle cracking than plants producing flat-round fruit. Within the generation with significant differences nearly half of plants producing globe shaped fruit had incidences of cuticle cracking over 30%, while less than 25% of the plants producing flat-round fruit had incidences greater than 30%. Eleven percent of the plants producing globe shaped fruit showed no cuticle cracking, indicating that the production of globe shaped fruit resistant to cuticle cracking is possible.

In our study it was found that increasing fruit size significantly increases the incidence and severity of cuticle cracking. Those results agree with the findings of Considine and Brown (1981), Janse (1985), and Koske et al. (1980). The resistance conferred by the symmetrical shape of globe shaped fruit could be offset by the large size, making size a more important factor in resistance to cuticle cracking than shape.

Results of the shape study provide further information about the variable nature of resistance in 'FM-9' and its hybrids. This cultigen is described as being "deep-round" with a "square appearance" (Leeper and Cox, 1986), and perhaps is more similar in shape to the globe fruit than

flat-round. Other characteristics of 'FM-9' may confer resistance, whereas the shape may be a detrimental factor under increasing environmental stress, making it less resistant.

Movement of water into the fruit is the source of turgor pressure placed on the epidermis, leading to cuticle cracking. During maturation of fruit from many tomato cultigens an abscission zone is formed in the pedicel. This jointed condition inhibits the flow of water into and out of the fruit. If an abscission zone is not formed, as in jointless pedicels, water is not restricted in movement into the fruit during maturation. This could result in great turgor pressure being placed upon the epidermis during periods of high rainfall. This study has shown that plants producing fruit with jointed pedicels tended to have lower incidences of cuticle cracking than plants producing fruit with jointless pedicels. However, significant differences were found for only one of 4 generations tested. Comparison on 2 near isogenic lines, differing by jointed versus jointless condition, indicated that the jointless condition by itself is not sufficient to significantly decrease resistance to cuticle cracking.

This study indicated that thickness of the epidermis and overlying cuticle layer is an important factor in resistance to cuticle cracking. Selection for a thicker layer may be made using light reflectance (L) of the fruit

(Hunter, 1975). Fruit size (small), shape (flat-round), and pedicel (jointed) should be taken into consideration when making selections for resistance to cuticle cracking.

CHAPTER 6
EFFECT OF ALTERING THE PLANT/ENVIRONMENT WATER RELATIONSHIP ON CUTICLE CRACKING

Introduction

Increased concentric and cuticle cracking of tomato fruit has been experimentally induced by pruning the plant to a single stem (Frazier, 1939) or removal of trusses of fruit (Ehret et al., 1993), respectively. These practices reduce the amount of transpirational tissue, which may act to increase the water flow to the remaining fruit. The former also increase fruit exposure, which could have other effects as well. Increased water uptake and transport to the fruit may also occur as soil water availability increases after a rainfall event. Reynard (1951) and Young (1947) reported the increase in incidence of cuticle cracking, as well as other types of cracking, after periods of heavy rainfall.

In a spring 1994 experiment there was a significant cultigen-by-harvest interaction for incidence and severity of cuticle cracking, which indicated that cultigens (cultivars, varieties, and breeding lines) (Soule, 1985) respond differently to either fruit load reduction (harvest)

or increased rainfall, or an interaction of the two. In studies prior to 1995, fruit load reduction due to harvesting and increases in rainfall occurred concurrently, making distinction of response impossible. Analysis of weather and cuticle cracking data from 1992 to 1995 has shown a positive correlation ($r=0.98$, $p \leq 0.01$) between amount of rainfall within two weeks prior to harvest and the incidence of cuticle cracking (Chapter 3). The objective of this study was to determine the effects of altering fruit load on the incidence and severity of cuticle cracking.

Materials And Methods

Cultigens Fla. 7181 and 'Suncoast' (Scott et al., 1985) were selected as susceptible lines, whereas Fla. 7497, 'FM-9' (Leeper and Cox, 1986), and 'C-28' (Moore, 1971) were chosen as resistant lines. 'Suncoast' and Fla. 7497 have globe shaped fruit (Appendix D) and differ in resistance to cuticle cracking. Fla. 7181 produces flat-round fruit with jointless pedicels (Appendix D). Fla. 7497 has an arthritic type pedicel in which the pedicel is swollen above the abscission zone and does not cleanly separate from it. 'FM-9' produces "deep-round" fruit with a "square appearance" (Leeper and Cox, 1986), with jointed pedicels. 'C-28'

produces flat-round fruit with jointed pedicels. Cultigens were seeded in the greenhouse in Black Beauty spent coal (Reed Minerals Div., Highland, IN) medium on 23 January and transplanted into Todd planter flats (3.8-cm^3 cell size) (Speedling, Sun City, FL) containing a 1:1 peat and vermiculite mixture on 8 February. Plants were set into the field at the Gulf Coast Research and Education Center, Bradenton, Fla. on 8 March in a randomized, complete-block design. Cultigens not used in this study were included in the field. Each of 4 blocks consisted of 15 plots, each containing 8 plants of an individual cultigen. Plots were randomly arranged in 6 rows per block. Mature-green and riper fruits were harvested twice on an individual plant basis. The first harvest (1995H1) occurred between 30 May and 5 June after 3 minor rainfall events within 2 weeks prior to harvest, resulting in 3.8 cm of rain. The second harvest (1995H2) occurred between 12 and 16 June after 6 rainfall events within 2 weeks prior to harvest, resulting in 14.3 cm of rain. Incidence and severity (Appendix A) of cuticle cracking were determined for each cultigen. Incidence and severity of cuticle cracking, fruit number and weight (yield), and fruit size (mass per fruit in kg) were analyzed by the PROC GLM and PROC CORR procedures of the Statistical Analysis System (SAS Institute, 1979). Fruit size, number of fruit, and yield are not independent of each other; therefore, effects on incidence and severity were

tested with individual regressions rather than by multiple regression (Gomez and Gomez, 1984).

An experiment designed to separate fruit load from rainfall effects was also conducted. Thirty plants each of cultigens 'C-28', Fla. 7497, and Fla. 7181 were set into the field at the Gulf Coast Research and Education Center, Bradenton, Fla. on 8 March in a completely randomized block design. Six weeks after planting, 10 plants per cultigen were given one of three treatments: one third of all set fruit were removed (medium load), two thirds of all set fruit were removed (low load), and no fruit were removed from control plants. All unset blossoms were removed from each treatment. All mature green fruits were harvested from all plants between 6 June and 10 June, following 6 rainfall events, resulting in 17.4cm of rain within 2 weeks prior to harvest. Incidence and severity (Appendix A) of cuticle cracking were determined for each cultigen and the data were transformed using the square root function to make the variances homogeneous (Zar, 1984). Incidence and severity of cuticle cracking, fruit number and weight (yield), and fruit size (mass per fruit in kg) were analyzed by PROC GLM and PROC CORR procedures of the Statistical Analysis System (SAS Institute, 1979). Fruit size, number of fruit, and yield were analyzed with individual regressions, due to non-independence of the factors.

Results

For 5 cultigens, fruit size and number of fruit significantly affected incidence of cuticle cracking (CC) at both harvests (Table 6-1). At harvest 1, fruit size accounted for 16% of the variance in incidence of CC, whereas number of fruit accounted for 8% of the variance in incidence of CC. Incidence of CC increased with increasing fruit size, and decreasing number of fruit (Table 6-1). At harvest 2, fruit size accounted for 33% of the variance in incidence of CC, whereas number of fruit accounted for 7% of the variance (Table 6-1). Again, incidence increased with increasing fruit size and decreasing number of fruit. Yield significantly affected incidence of CC at harvest 1, but accounted for only 3% of the variance. Incidence decreased as yield increased. Severity was significantly affected by fruit size and number of fruit at harvest 2 (Table 6-2). As fruit size increased, severity increased, accounting for 17% of the variance in severity. As the number of fruit increased, severity decreased, accounting for 6% of the variance in severity (Table 6-2).

In the study to test fruit load effects on incidence and severity of CC, cultigen differences had a greater effect on incidence and severity of CC than fruit load treatments (Table 6-3).

Table 6-1. Regression analysis for incidence of cuticle cracking on number of fruit, fruit size, and yield over 5 cultigens for 2 harvests.

Parameter	Estimate	T for H0: Parameter=0	Pr > |T|	r^2
HARVEST 1				
INTERCEPT	-0.14	-2.64	0.009	0.16
SIZE	0.77	5.26	<0.001	
INTERCEPT	0.19	5.30	<0.001	0.03
YIELD	-0.02	-2.19	0.03	
INTERCEPT	0.22	6.60	<0.001	0.08
NUMBER OF FRUIT	-0.01	-3.41	<0.001	
HARVEST 2				
INTERCEPT	-0.10	-1.51	0.13	0.33
SIZE	1.84	8.60	<0.001	
INTERCEPT	0.36	6.47	<0.001	0.01
YIELD	0.01	1.43	0.15	
INTERCEPT	0.59	10.47	<0.001	0.07
TOTAL	-0.01	-3.21	0.002	

Table 6-2. Regression analysis for severity of cuticle cracking on number of fruit, fruit size, and yield over 5 cultigens for 2 harvests.

Parameter	Estimate	T for H0: Parameter=0	Pr > |T|	r^2
HARVEST 1				
INTERCEPT	1.01	4.72	<0.001	0.03
SIZE	0.54	1.08	0.29	
INTERCEPT	1.30	11.26	<0.001	0.01
YIELD	-0.02	-0.74	0.46	
INTERCEPT	1.30	12.51	<0.001	0.02
NUMBER OF FRUIT	-0.01	-0.94	0.35	
HARVEST 2				
INTERCEPT	1.60	16.93	<0.001	0.17
SIZE	1.47	4.95	<0.001	
INTERCEPT	2.01	28.36	<0.0001	0.003
YIELD	0.01	0.59	0.56	
INTERCEPT	2.22	31.21	<0.001	0.06
NUMBER OF FRUIT	-0.01	-2.69	0.008	

Table 6-3. Analysis of variance for incidence and severity of cuticle cracking for fruit load experiment.

Source	df	MS	P value
INCIDENCE			
Cultigen	2	4.68	<0.01
Treatment	2	0.01	0.56
Cultigen*Treatment	4	0.05	0.08
Error	76	0.02	
SEVERITY			
Cultigen	2	0.12	0.04
Treatment	2	0.01	0.79
Cultigen*Treatment	4	0.14	<0.01
Error	44	0.03	

Fruit load treatments did not significantly affect either incidence or severity of CC (Table 6-3) over all cultigens or for any individual cultigen except Fla. 7497 (Table 6-4).

Over all cultigens the trend was for incidence to increase with each decrease in fruit load (treatment), whereas severity remained fairly constant (Table 6-4). Significant cultigen by treatment interaction effects for severity were due to treatment differences for cultigen Fla. 7497. For Fla. 7497, medium load treatment had a significantly lower severity than either other fruit load levels (Table 6-4). The difference between treatments was not significant for 'C-28' or Fla. 7181. Medium load treatments reduced the number of fruit harvested (NFH) by 7-26%. The reduction of NFH by medium load treatments was significant only for Fla. 7181. Low load treatments reduced NFH by 28-38% (Table 6-4). The reduction of NFH by low load treatments was significant for 'C-28' and Fla. 7181.

Yield was reduced by 0-25% by medium load treatments, but was significant only over all cultigens. Low load treatments reduced yield by 19-31%, and were significant only over all cultigens (Table 6-4). Fruit size increased significantly over all treatments for all cultigens combined, and for 'C-28' alone. (Table 6-4).

Table 6-4. Cultigen and treatment effects on fruit load, yield, and incidence and severity of cuticle cracking[z].

OVER ALL CULTIGENS

	CONTROL	MEDIUM LOAD	LOW LOAD
Number of fruit	25.9a	21.0b(19)[y]	17.4b(33)
Yield (kg)	4.0a	3.3b(18)	3.0b(25)
Size of Fruit (kg)	0.15b	0.16b	0.17a
Incidence	26.3	27.7	33.1ns
Severity	3.4	3.1	3.3ns

'C-28'

	CONTROL	MEDIUM LOAD	LOW LOAD
Number of Fruit	33.3a	28.7ab(14)	23.9b(28)
Yield (kg)	4.3	3.8(12)	3.5(19)ns
Size of Fruit (kg)	0.13b	0.13ab	0.15a
Incidence	5.1	2.5	6.5ns
Severity	2.8	3.0	3.0ns

Fla. 7497

	CONTROL	MEDIUM LOAD	LOW LOAD
Number of Fruit	14.8a	13.7a(7)	9.2a(38)
Yield (kg)	2.0	2.1(0)	1.4(30)ns
Size of Fruit (kg)	0.14	0.15	0.15ns
Incidence	13.3	18.2	12.3ns
Severity	3.6a	2.4b	3.5a

Fla. 7181

	CONTROL	MEDIUM LOAD	LOW LOAD
Number of Fruit	27.6a	20.5b(26)	17.3b(37)
Yield (kg)	5.5	4.1(25)	3.8(31)ns
Size of Fruit (kg)	0.20	0.20	0.22ns
Incidence	80.1	79.2	90.0ns
Severity	3.5	3.9	3.2ns

[z] Mean separation in rows by Duncan's multiple range test at $p \leq 0.05$, ns=not significantly different

[y] (% Reduction from control)

Treatment was partitioned into components and tested for individual effects. Yield and fruit size had significant effects on incidence of cuticle cracking (Table 6-5). As yield increased, both incidence and severity increased, accounting for 6% and 8% of the variance, respectively. As fruit size increased, incidence and severity of CC increased, accounting for 47% and 17% of the variance, respectively.

Table 6-5. Regression analysis for incidence and severity of cuticle cracking on number of fruit, fruit size, and yield in fruit load experiment.

Parameter	Estimate	T for H0: Parameter=0	Pr > |T|	r^2
INCIDENCE				
INTERCEPT	-0.66	-5.20	<0.001	0.47
SIZE	2.94	8.57	<0.001	
INTERCEPT	0.22	2.52	0.01	0.06
YIELD	0.02	2.20	0.03	
INTERCEPT	0.52	5.46	<0.001	0.02
NUMBER OF FRUIT	-0.01	-1.43	0.16	
SEVERITY				
INTERCEPT	1.42	10.83	<0.001	0.14
SIZE	0.95	2.86	0.01	
INTERCEPT	1.66	25.32	<0.001	0.08
YIELD	0.02	2.17	0.03	
INTERCEPT	1.70	21.16	<0.001	0.03
NUMBER OF FRUIT	0.004	1.26	0.21	

Table 6-6. Pearson correlation coefficients and probabilities for yield and cuticle cracking measures over 3 cultigens (1995).

	NUMBER[z]	YIELD[y]	SIZE[x]
INCIDENCE	-0.08 p=0.46	0.31 p=0.004	0.72 p<0.001
SEVERITY	0.15 p=0.29	0.27 p=0.05	0.37 p=0.007
SIZE	-0.11 p=0.32	0.39 p=0.0002	

[z] Total number of fruit harvested per plant
[y] Total weight of fruit harvested per plant
[x] Weight (kg) per fruit

Discussion

The objective of this study was to determine the effect of changing the water gradient between fruit and soil on incidence and severity of cuticle cracking (CC), by reducing fruit load independently of changes in rainfall. The first phase of the study indicated a significant effect of reduction in fruit load due to harvest, as measured by numbers or weight harvested, and increased incidence of CC; and increasing incidence of CC due to increased fruit size. Fruit size explained more of the variation in incidence than number of fruit, thus indicating that fruit size is more important in influencing resistance to CC than number of fruit at harvest. Severity of CC does not appear to be as

sensitive as incidence to changes in fruit load, with only fruit size and number of fruit having significant effects at harvest 2. As with incidence, fruit size explained more of the variation in severity than number of fruit.

Attempts to test the effects of reduction in fruit load did not show significant increases in incidence or severity of CC. Treatments reduced fruit load, but not enough to significantly affect incidence or severity of CC. Medium load treatments resulted in 7-26% reduction in number of fruit harvested rather than the expected 33% reduction. Low load treatments resulted in 28-37% reduction in number of fruit harvested rather than the expected 67% reduction. Yield was reduced less than number of fruit due to the increase in fruit size. In this part of the study fruit size and yield were significant factors affecting incidence and severity of CC, with fruit size explaining more of the variation in each.

Yield, number of fruit at harvest, and size of fruit appeared to be important in determining the incidence and severity of CC in tomato fruit, with fruit size being most important. Increased numbers of fruit at harvest leads to more fruit to which water may be distributed, sending less water to, and placing less stress on, any individual fruit. The incidence of CC significantly increased as fruit size increased. These results agree with those of Janse (1985) and Koske et al. (1980). Smaller fruit have a greater surface area to volume ratio, providing a higher proportion

of skin over which to distribute stress than large fruit (Considine and Brown, 1981). Ehret et al. (1993) found that fruit size was not related to the severity of CC in tomatoes, as did our study.

CHAPTER 7
SUMMARY AND SUGGESTIONS FOR FURTHER RESEARCH

Cuticle cracking (rain check) is a disorder affecting tomato fruit in which stress placed on the epidermis by an influx of water causes the cuticle layer to crack. This disorder degrades the appearance of the fruit and reduces shelf life by compromising the integrity of the epidermis, thus allowing increased water loss and invasion by pathogens. The objectives of this study were to 1) investigate the mode of inheritance of resistance to cuticle cracking by means of diallel studies, and 2) identify anatomical and/or physiological factors of the plant and or fruit that are associated with resistance to this disorder.

Through the course of this study two factors of importance to any study of cuticle cracking became apparent: 1) there is a large environmental effect on the incidence of cuticle cracking and 2) cultigens do not differ significantly in severity of cuticle cracking; therefore, incidence is a better indicator of resistance.

This study has shown that there is a direct and strong correlation between the amount of rain within 2 weeks prior to harvest and the incidence of cuticle cracking as compared to the amount of rain within 1 week of harvest and during the full growing season prior to harvest. High rainfall

made even the most resistant lines crack to some degree, and low rainfall induced only minimal cuticle cracking in susceptible lines. Therefore, if possible, testing and selection for cuticle cracking resistance should take place within 2 weeks following a moderate (7-10 cm) rainfall.

Severity of cuticle cracking did not vary significantly between cultigens. It seems that once the cuticle has cracked, sufficient pressure on the epidermis has been released and no further cracking occurs. The severity of cuticle cracking is more a function of environmental stress than cultigen differences. Incidence of cuticle cracking does differ significantly between cultigens and significantly increases with increased environmental pressure. Therefore, incidence was the best measure of resistance to cuticle cracking suggested by these studies.

One of the main questions a plant breeder must answer when undertaking a project to improve the performance of a crop is whether there is sufficient genetic variation within the available germplasm to allow improvement of the character in question (Dudley and Moll, 1969). In this study 11 cultigens of *Lycopersicon esculentum*, Mill. from diverse genetic backgrounds were screened for resistance to cuticle cracking. As a result of the screening and further studies, several key factors involving selection for resistance to cuticle cracking were determined. First, in answer to Dudley and Moll's question, the range of resistance to incidence of cuticle cracking was wide for the

population tested. Considering that the tested lines ranged from unimproved breeding lines to commercial varieties it can be concluded that a great deal of genetic variation in resistance to cuticle cracking exists in *L. esculentum*, Mill., making improvement possible through breeding efforts.

A second factor to consider during selection for resistance to cuticle cracking is that susceptible cultigens showed more variation in response to environmental stress than did resistant cultigens. Greater variation in cultigens susceptible to radial cracking than cultigens resistant to radial cracking was found for tomato by Reynard (1951), and for peppers by Johnson and Knavel (1990). Plants from nonsegregating populations of susceptible cultigens often show a bimodal distribution in terms of incidence of cuticle cracking. Symptomless 'escape' plants and plants showing little or no cuticle cracking, can make a susceptible cultigen appear more resistant. Evaluation of resistance to cuticle cracking at the inbred or F_1 generation should be based on the performance of the population as a whole, rather than on individual plant incidence. Progeny testing of 'resistant' plants in F_2 and other early generations should be done to determine the true nature of the resistance.

The environmental effect on incidence of cuticle cracking is high, as mentioned previously. Incidence of cuticle cracking in susceptible lines increased by a greater extent as rainfall increased, than did incidence in

resistant cultigens, which resulted in a significant environment by cultigen interaction. Under heavy rainfall, even the most resistant cultigens can be induced to a fair amount of cuticle cracking, making the distinction between resistant and susceptible less clear. Whenever possible, selection for resistance to cuticle cracking should take place following a moderate amount of rainfall for optimal distinction between resistance and susceptibility.

Attempts to induce cuticle cracking without altering irrigation or rainfall were not successful. Leaves and/or fruit were removed from plants to expose fruit to intense sunlight and increase the amount of water being distributed to the remaining fruit. Removal of leaves was not as severe as in the studies by Ehret et al. (1993) and Frazier (1936) and resulted in no significant difference in cuticle cracking between pruned plants and control plants. Removal of fruit to increase water distribution to remaining fruit appeared to induce the treated plants to produce more fruit on later trusses, necessitating more than one pruning during fruit set.

Genetic studies of the inheritance of resistance to cuticle cracking in tomato had not been done prior to this study. A genetic study of radial cracking and scarring (similar to cuticle cracking) in peppers (Johnson and Knavel, 1990) indicated that genetic effects in the form of overdominance in the direction of increased cracking were significant, with additive effects significant in some

families. Reynard (1951) found that dominant genes for radial cracking increased the incidence of cracking in tomato. In this study, additive gene effects were significant over all environments tested, with dominance effects in the direction of reduced cuticle cracking becoming significant under high stress conditions. Significant dominance effects in 1994 were in the form of partial to overdominance in the direction of increasing resistance to cuticle cracking in resistant by resistant crosses, and partial to complete dominance in resistant by susceptible crosses. Overdominance and differences in performance of resistant lines and their progeny indicate that the resistant lines tested may be under different genetic control and transgressive segregation for improved resistance from resistant by resistant cultigens may be possible. Dominant alleles increased resistance to cuticle cracking under low to moderate rainfall conditions. This is in contrast to the genetic control of radial cracking, in which dominant alleles decreased resistance (Reynard, 1951). Under high rainfall conditions, equal or varying numbers of dominant alleles increased or decreased resistance, depending on the cross. If possible, selection for resistance to cuticle cracking should be done under moderate environmental stress to reduce the dominance effects. Narrow sense and broad sense heritabilities ranged from 0.45 to 0.69, and 0.62 to 0.89, respectively, and increased from one harvest to the next within each year due to increasing

rainfall. No epistatic interactions were detected in this study. Maternal effects were not significant over most resistant by susceptible parental combinations, but significant differences were found between F_1 hybrids of 'C-28' x Fla. 7181 at harvest 3 in 1994. In general, hybrids with the resistant parent as female had lower, but not significantly different, incidence of cuticle cracking than the reciprocal. Further diallel studies, possibly with a different set of cultigens should be done to clarify the question of maternal effects and importance of SCA.

Cuticle cracking of tomato fruit occurs as a result of a rapid or uneven increase of turgor pressure placed upon the cuticle and epidermal wall (epicarp) (Janse, 1985; Hayman, 1987; den Outer and van Veenendaal, 1987). The epicarp must be strong enough to resist cracking, while at the same time have sufficient extensibility to allow for expansion. A thick epidermal wall and/or cuticular layer would provide strength for resistance to cracking. Since the boundary between those two layers is not easily distinguished microscopically in tomato, they were measured as one unit (epicarp). In this study it was found that the 3 cultigens most resistant to cuticle cracking had significantly thicker epicarp layers than the two susceptible cultigens. This is in agreement with the results of Borowiak and Habdas (1988) for mechanical injury in tomatoes, but in contrast to the results of den Outer and van Veenendaal (1987) for cuticle cracking in a single

tomato cultigen. This study compared epicarp measures above locules for different cultigens, whereas that of den Outer and van Veenendaal compared epicarp measures above carpel walls between cracked and non-cracked fruit of one cultigen. A study comparing epicarp measures above locules and above carpel walls within one cultigen is needed to clarify the discrepancy.

Fruit from cultigens resistant to cuticle cracking have less elongated epidermal cells than fruit from cultigens susceptible to cuticle cracking. Den Outer and van Veenendaal (1987) found similar results. The more rounded shape potentially distributes pressure more evenly throughout the cell and to the overlying wall and cuticle, reducing the pressure on any one area (Considine and Brown, 1981), thus reducing the potential for cracking.

Cuticle cracks originated in the region of cell junctions where waxy cutin 'pegs' extend between epidermal cells. The pegs appear to be less electron dense, suggesting a difference in structure or composition from the cuticle overlying the tangential walls of the epidermal cells. This may represent the point of weakness where cuticle cracking may occur under the stress of turgor pressure.

Thickness of the epicarp showed a significant negative correlation ($r=-0.43$, $p<0.001$) to the light reflectance (L) of the fruit surface. Light reflectance may be used to assist in identification of resistance due to thicker

epicarp when the environment is not conducive to cuticle cracking, when comparing fruit grown under the same environmental conditions and of the same size.

Fruit shape was found to significantly affect the incidence of cuticle cracking in one of four segregating populations. In the population with significant shape effects, plants producing globe shaped fruit had higher incidences of cuticle cracking than plants producing flat-round fruit. Populations with nonsignificant shape effects showed the same trend of plants producing globe shaped fruit having higher incidences than plants producing flat-round fruit. This is in contrast to the theoretical considerations of Considine and Brown (1981), who suggested that globe shaped fruit would better distribute the forces from turgor pressure and be more resistant to cracking than irregular shaped fruit. This suggests that factors besides shape are more important in determining resistance to cuticle cracking in tomato.

For one of three populations segregating for jointed or jointless pedicels, plants with jointless pedicels had higher incidences of cuticle cracking than plants with jointed pedicels. Fruit with jointless pedicels may be less able to restrict water influx during maturation, making them less resistant to cuticle cracking. This effect on resistance appears to be minor, and can be overcome by other factors.

Fruit size, number of fruit at harvest, and yield appear to affect incidence of cuticle cracking, with fruit size being the most important factor, accounting for 16-33% of the variance in incidence of cuticle cracking as compared to 7-8% and 3% for number of fruit harvested and yield, respectively. As fruit size increased, the incidence of cuticle cracking significantly increased. This result has been shown in previous studies with tomato (Janse, 1985; Koske et al., 1980) and fit into the theoretical consideration that smaller fruit have a greater surface area to volume ratio over which to distribute the forces from turgor pressure (Considine and Brown, 1981).

APPENDIX A
CUTICLE CRACKING SEVERITY RATING SCALE

A-1. Description of severity of cuticle cracking rating scale.

RATING	VISIBLE APPEARANCE
0	GLOSSY, NO CRACKS
1	DULL, HAIR-LIKE CRACKS, NO LESIONS VISIBLE
2	$\leq$12.5% OF SHOULDER COVERED WITH LESIONS
3	>12.5% $\leq$ 25% OF SHOULDER COVERED WITH LESIONS
4	>25% $\leq$ 50% OF SHOULDER COVERED WITH LESIONS
5	>50% $\leq$ 75% OF SHOULDER COVERED WITH LESIONS
6	>75% $\leq$ 87.5% OF SHOULDER COVERED WITH LESIONS
7	>87.5% < 100% OF SHOULDER COVERED WITH LESIONS
8	100% OF SHOULDER COVERED WITH LESIONS
9	LESIONS EXTEND BEYOND THE SHOULDER
10	FRUIT TOTALLY COVERED WITH LESIONS

A-2. Illustration of severity of cuticle cracking rating scale.

APPENDIX B
TOMATO CULTIGENS USED IN RAIN CHECK EXPERIMENTS

B-1. Tomato cultigens grown in Spring 1992 Experiment.

PEDIGREE	SEED SOURCE
A. Resistant Sources[z]	
NC50-7	P1360
Fla. 7171	880024-BK
Campbell 28 (C-28)	Sp 91
Solar Set	Asgrow
Fresh Market 9 (FM-9)	Sp 87
(Fla. 7232 X Fla. 7244) F_5	914052-1
(Fla. 7220 X Fla. 7228) F_7	914208-1
{Fla. 7241 X [(Fla. 7060 X H7998) X Fla. 7165]M3} F_4	913418-1
{Fla. 7217D X [(Fla. 7060 X H7998) X Fla. 7165]M5} F_5	914081-1
(Fla. 7065 X Fla. 7156) F_4	913011-1
(Fla. 7178 X Fla. 7237) F_4	913075-1
<Fla. 7178 X {Fla. 7182 X [Fla. 7067 X (Fla. 645 X H7997)]}> F_6	910338-1
NC8276	86E101S
B. Susceptible Sources	
Suncoast	Sp 86
Fla. 7181	854049-4
Fla. 7060	880023-BK
FL1B	Sp 80
C. Misc.	
(Fla. 7236 X CL5915) F_3	914286-1
(Fla. 7317 X Fla. 7319) F_4	914340-1

[z] Pedigree source designations are based upon previous observations

B-1. Tomato cultigens grown in Spring 1992 Experiment (CONT'D).

PEDIGREE	SEED SOURCE
D. Globes - low check[z]	
(Fla. 7220 X Fla. 7228) F_6	910270-1
(Fla. 7193 X Fla. 7228) F_6	910277-1
(Fla. 7232B X Fla. 7321) F_4	910281-1
<Fla. 7294 X {Fla. 7198 X [HAYSLIP X (Fla. 7067-A X H7983)]}> F_4	910463-1
<(Fla. 7182 X Fla. 7179) X {[Fla. 7060 X (BURGIS X H7998)] X PRI I3} M6> F_4 (Fla. 7497)	910529-1
E. Lenticel types	
{Fla. 7065 X [Fla. 7057 X (HAYSLIP X LA716)]} F_5	864401-1
{Fla. 7067 X [Fla. 7057 X (HAYSLIP X LA716)]} F_3	854693-1
[Fla. 7057 X (HAYSLIP X LA 716)]-II1-3-3	850704-3S
[Fla. 7057 X (HAYSLIP X LA 716)]-I1-492E228S	844656-4
[Fla. 7057 X (HAYSLIP X LA 716)]-II1-3	844658-3

[z] Pedigree source designations are based upon previous observations

B-2. Tomato cultigens grown in Spring 1993 Experiment.

PEDIGREE	SEED SOURCE
A. Parents	
C-28	Sp 91
FM-9	Sp 87
Suncoast	Sp 86
Fla. 7181	854049-4
Fla. 7497	910529-1
[Fla. 7411B X (Fla. 7395 X LA1959)]-8 (Wild)	926055-BK
B. F_1 Hybrids	
C-28 X FM-9	6050 X 6051
C-28 X Fla. 7181	6050 X 6052
C-28 X Suncoast	6050 X 6053
C-28 X Fla. 7497	6050 X 6054
C-28 X Wild	6050 X 6055
FM-9 X C-28	6051 X 6050
FM-9 X Fla. 7181	6051 X 6052
FM-9 X Suncoast	6051 X 6053
FM-9 X Fla. 7497	6051 X 6054
FM-9 X Wild	6051 X 6055
Fla. 7181 X C-28	6052 X 6050
Fla. 7181 X FM-9	6052 X 6051
Fla. 7181 X Suncoast	6052 X 6053
Fla. 7181 X Fla. 7497	6052 X 6054
Fla. 7181 X Wild	6052 X 6055
Suncoast X C-28	6053 X 6050
Suncoast X FM-9	6053 X 6051
Suncoast X Fla. 7181	6053 X 6052
Suncoast X Fla. 7497	6053 X 6054
Suncoast X Wild	6053 X 6055
Fla. 7497 X C-28	6054 X 6050
Fla. 7497 X FM-9	6054 X 6051
Fla. 7497 X Fla. 7181	6054 X 6052
Fla. 7497 X Suncoast	6054 X 6053
Fla. 7497 X Wild	6054 X 6055
Wild X C-28	6055 X 6050
Wild X FM-9	6055 X 6051
Wild X Fla. 7181	6055 X 6052
Wild X Suncoast	6055 X 6053
Wild X Fla. 7497	6055 X 6054

B-3. Tomato cultigens grown in 1994 and 1995 experiments.

1994 SEED SOURCE	PEDIGREE	1995 SEED SOURCE
A. Parents		
Sp 91	C-28	Sp 91
Sp 87	FM-9	Sp 82
Sp 86	Suncoast (SC)	Sp 94
854049-4	Fla. 7181	94E504-BK
910529-1	Fla. 7497	910529-1
B. F1		
6050 X 6051	C-28 X FM-9	942098 X 942094
6050 X 6052	C-28 X Fla. 7181	942098 X 942095
6050 X 6053	C-28 X SC	942098 X 942084
6050 X 6054	C-28 X Fla. 7497	926050 X 926054
6051 X 6050	FM-9 X C-28	
6051 X 6052	FM-9 X Fla. 7181	932053 X 932054
6051 X 6053	FM-9 X SC	942094 X 942084
6051 X 6054	FM-9 X Fla. 7497	942094 X 942099
6052 X 6050	Fla. 7181 X C-28	
6052 X 6051	Fla. 7181 X FM-9	
6052 X 6053	Fla. 7181 X SC	
6052 X 6054	Fla. 7181 X Fla. 7497	
6053 X 6050	SC X C-28	
6053 X 6051	SC X FM-9	
6053 X 6052	SC X Fla. 7181	932055 X 932024
6053 X 6054	SC X Fla. 7497	
6054 X 6050	Fla. 7497 X C-28	
6054 X 6051	Fla. 7497 X FM-9	
6054 X 6052	Fla. 7497 X Fla. 7181	926054 X 926052
6054 X 6053	Fla. 7497 X SC	926054 X 926053

B-4. Cultigens of segregating generations grown in 1995.

PEDIGREE	SEED SOURCE
A. F_2	
(C-28 x Fla. 7181) x (C-28 x Fla. 7181)	95E5085-BK
(C-28 x Suncoast) x (C-28 x Suncoast)	95E5095-BK
(C-28 x Fla. 7497) x (C-28 x Fla. 7497)	95E5105-BK
(Fla. 7181 x Fla. 7497) x (Fla. 7181 x Fla. 7497)	95E5205-BK
B. BC	
C-28 x (C-28 x Fla. 7181)	932052x93E2325
C-28 x (C-28 x Suncoast)	932052x93E2335
C-28 x (C-28 x Fla. 7497)	932051x93E2345
Fla. 7181 x (C-28 x Fla. 7181)	932054x93E2325
Fla. 7181 x (Fla. 7181 x Suncoast)	932054x93E2435
Fla. 7181 x (Fla. 7181 x Fla. 7497)	932054x93E2445
Suncoast x (C-28 x Suncoast)	932055x93E2335
Fla. 7497 x (C-28 x Fla. 7497)	932056x93E2345
Fla. 7497 x (Fla. 7497 x Fla. 7181)	932056x93E2445

APPENDIX C
MID-PARENT VALUES FOR 1994 AND 1995 DIALLELS

C-1. Incidence of cuticle cracking (1994).

PARENT	C-28	FM-9	FLA. 7497	SUNCOAST	FLA. 7181
Harvest 1					
C-28	0.1	0.6	0.2	1.6	11.0
FM-9		1.0	0.6	2.0	11.4
FLA. 7497			0.3	1.7	11.0
SUNCOAST				3.1	12.4
FLA. 7181					21.8
Harvest 2					
C-28	3.4	7.9	6.6	18.3	29.6
FM-9		12.4	11.2	22.8	34.0
FLA. 7497			9.9	21.6	32.8
SUNCOAST				33.2	44.4
FLA. 7181					55.7
Harvest 3					
C-28	15.0	18.8	23.7	25.4	40.0
FM-9		22.6	27.5	29.2	43.8
FLA. 7497			32.4	34.1	48.6
SUNCOAST				35.8	50.4
FLA. 7181					64.9

C-2. Severity of cuticle cracking (1994).

PARENT	C-28	FM-9	FLA. 7497	SUNCOAST	FLA. 7181
HARVEST 1					
C-28	6.00	4.50	6.00	4.75	4.96
FM-9		3.00	4.50	3.25	3.46
FLA. 7497			6.00	4.75	4.96
SUNCOAST				3.50	3.70
FLA. 7181					3.91
HARVEST 2					
C-28	2.00	2.11	2.36	2.56	2.74
FM-9		2.22	2.47	2.68	2.85
FLA. 7497			2.72	2.92	3.10
SUNCOAST				3.13	3.30
FLA. 7181					3.48
HARVEST 3					
C-28	2.71	2.80	3.34	3.09	3.37
FM-9		2.88	3.42	3.18	3.46
FLA. 7497			3.97	3.72	4.00
SUNCOAST				3.47	3.75
FLA. 7181					4.03

C-3. Index of cuticle cracking (1994).

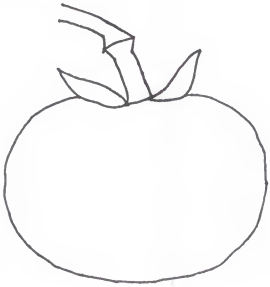
PARENT	C-28	FM-9	FLA. 7497	SUNCOAST	FLA. 7181
HARVEST 1					
C-28	0.01	0.02	0.02	0.08	0.46
FM-9		0.04	0.04	0.09	0.48
FLA. 7497			0.03	0.08	0.47
SUNCOAST				0.14	0.52
FLA. 7181					0.91
HARVEST 2					
C-28	0.07	0.18	0.18	0.56	1.02
FM-9		0.29	0.28	0.66	1.14
FLA. 7497			0.28	0.66	1.13
SUNCOAST				1.04	1.98
FLA. 7181					
HARVEST 3					
C-28	0.42	0.56	0.86	0.82	1.55
FM-9		0.69	1.00	0.96	1.68
FLA. 7497			1.30	1.26	1.99
SUNCOAST				1.23	1.96
FLA. 7181					2.68

C-4. Incidence of cuticle cracking (1995).

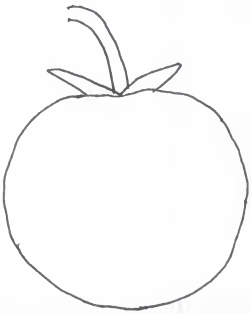
PARENT	C-28	FM-9	FLA. 7497	SUNCOAST	FLA. 7181
HARVEST 1					
C-28	0.4	4.6	1.8	9.6	4.1
FM-9		8.8	6.0	13.8	8.3
FLA. 7497			3.2	11.0	5.5
SUNCOAST				18.7	13.3
FLA. 7181					7.8
HARVEST 2					
C-28	7.0	11.2	16.6	21.0	31.4
FM-9		15.4	20.8	25.2	35.6
FLA. 7497			26.1	30.5	40.9
SUNCOAST				34.9	45.3
FLA. 7181					55.7

APPENDIX D
FRUIT SHAPE AND PEDICEL TYPES

1. Flat-round, Jointed Pedicel



2. Globe, Jointless Pedicel



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Cheryld L. Whaley Emmons is the oldest daughter of Charles and Wanda Whaley of Richland, New York. Her bachelor's degree in science, majoring in biology, was earned in 1981 from Siena College in Loudonville, New York. In 1982 Cheryld entered graduate study at Bowling Green State University, at Bowling Green, Ohio. The topic of her thesis study was effects of acidified mist on *Liriodendron tulipifera*, supervised by Dr. Reginald Noble. Her Master of Science degree was earned in 1984, after which Cheryld began a 2-year career in research for Campbell's Institute for Research and Technology. Upon moving to Florida in 1987, she met Dr. John Scott at the Gulf Coast Research and Education Center, whose research inspired her to pursue a Ph.D. in plant breeding and genetics at the University of Florida.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Professor of Horticultural Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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